THE UNIVERSITY OF ALBERTA

Effect of mowing on carbohydrate reserves and regeneration of western snowberry (Symphoricarpos occidentalis Hook.)

by

© Barry W. Adams

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(SIGNED) Barry Adams

PERMANENT ADDRESS:

9919 - 77 St.

Edmonton, Alberta

DATED Sept 9 1983

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Effect of mowing on carbohydrate reserves and regeneration of western snowberry (Symphoricarpos occidentalis Hook.) submitted by Barry W. Adams in partial fulfilment of the requirements for the degree of Master of Science in Range Management.

Arthur W. Bailey

Supervisor

Ethel Ann Clark

Kenneth A. Higginbottom

Date September 9, 1983

Abstract

A study was conducted in the aspen parkland of central Alberta to determine the effect of season and frequency of mowing on non-structural carbohydrate (NSC) reserves and regeneration of western snowberry. Eight treatment combinations were designed including all possible combinations of single, double and triple mowing May 8, June 24 and August 13, 1981.

The seasonal low in NSC in the root crown came later than was previously suspected, and was associated with the stage of 2/3 shoot elongation. Spring cutting caused a greater and more prolonged depletion of NSC reserves than was apparent in the control. In spite of this, recharge of root crown NSC reserves began six weeks after resprouting commenced, when new suckers had produced 11 leaf pairs. Root recharge was complete when flowers opened on new suckers, nine weeks after sprouting was first observed.

NSC reserves and etiolated growth (EG) were compared as measures of resprouting potential. NSC reserves declined as frequency of cutting increased and as cutting dates became progressively later. Autumn EG reserves showed progressive reductions with increased frequency of cutting. However, only the single August cut showed a reduction in EG due to the season of cutting. EG reserves were disproportionately reduced compared to the reduction in NSC after late cutting. The significant reduction in EG reserves with late cutting was attributed to the effect of frost injury to buds released after the single late-summer cut. Once the late released sprouts were frost injured, a higher energy cost may have been incurred in releasing buds of lower developmental status.

In 1982, aerial biomass of western snowberry was proportional to the weight of stem material that regrew, after mowing, in 1981. The plants initiated growth in the spring of 1982 from stems that had regrown in 1981, or from the stump in those treatments where no regrowth was produced after mowing. Though forage production was trebled in the triple mowed stands and the vigour of western snowberry was reduced to 20% of

the control, it was clear that short term gains would soon be lost to shrub regeneration in the foreseeable future.

Winter injury of vegetative buds that were released late in the season was an important finding for two reasons. First, it may be possible to reduce the regenerative potential of western snowberry by depleting the supply of vegetative buds with late-summer cutting. Secondly, late-summer cutting may favour the production of short shoots which tend to render woody plants more susceptible to phenoxy herbicides.

To control western snowberry, shrub stands should first be pre-stressed, preferably by late-summer mowing, or by spring burning if site conditions limit mechanical means. Secondary treatment with 2,4-D ester should then be timed with phenological stages that coincide with recharge of root reserves. In this study the recharge of root reserves was defined by the interval in which suckers produced after mowing possessed 11 leaf pairs and up to the time of flowering.

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1. Introduction

Symphoricarpos occidentalis Hook., commonly known as western snowberry, is an erect deciduous shrub, common to the Northern Great Plains of North America. Due to its strong rhizomatous nature, western snowberry typically assumes a clonal growth habit. In the aspen parkland, western snowberry spreads into native grasslands (Pelton 1953), creating a barrier to grazing and reducing forage production. Western snowberry is particularly unpalatable to cattle, although sheep and goats find it somewhat more acceptable. Past research has established that western snowberry is a difficult shrub to control on native rangeland.

If snowberry regeneration could be controlled, the potential for increased forage production would be quite high, because western snowberry tends to claim the most productive range sites (Wheeler 1976). In most stands, existing forage plants will be present and able to respond to release from shrub competition (Pelton 1953). Single and multiple control treatments (spray, burn, mow, graze) have produced variable, but generally short lived, control.

1.1 Experimental Objectives

The potential to resprout in woody plants is primarily due to:

a. substrate in the form of nonstructural carbohydrate (NSC) to supply the requirements of growth (Smith 1969), and

b. vegetative buds which may differentiate into new shoots (Schier 1976).

In western snowberry, a rhizomatous growth habit indicates a supply of NSC and vegetative buds and is a major factor accounting for the substantial regenerative potential of this shrub.

Smith (1969) stated that carbohydrate reserves are strongly related to regenerative potential. The traditional approach to brush control has been to deplete NSC

reserves (Launchbaugh and Owensby 1978) by varying the season and frequency of defoliation. According to this approach, the first step would be to define seasonal trends in root reserves, and the second would be to define the regrowth interval required for the plant to recover its root reserves after top removal. Cutting during the seasonal low, and then repeatedly, as new growth further reduces reserves, could significantly reduce NSC.

In more recent times, vegetative buds have been considered as a component of regenerative potential (Shier 1976). With the advent of phenoxy herbicides, researchers have investigated the potential to "kill underground reservoirs" of buds (Garrison 1972). In addition to herbicides, strategically timed defoliation may also reduce regrowth potential by enhancing winter damage to vegetative buds. FitzGerald (1982) concluded that the greater control of aspen regrowth with late versus early-season grazing may have resulted from winter injury to vegetative buds. He hypothesized that late grazing may have interfered with dormancy induction and prevented adequate winter hardening.

Given that the regenerative potential of western snowberry resides with the root system, the goal of the present study was to devise a pre-treatment strategy designed to maximize physiological stress on the underground organs of the shrub. Since 2,4-D ester will produce an excellent top kill with timely application (Friesen *et al*. 1965), the pre-treatment(s) would be aimed at reducing the regenerative potential of roots prior to a herbicide treatment.

Since a physiological study was being undertaken in an uncontrolled environment, the monitoring of selected environmental parameters was necessary.

The principal objectives of this study were as follows:

1. To determine:

   a. the annual NSC reserve cycle of western snowberry, and

   b. the effect of spring mowing on the seasonal reserve cycle.

2. To determine the effect of season and frequency of mowing:

   a. on phenology, fall sprouting reserves and stand regeneration,

   b. on shrub and herbage production.

3. To determine the effect of mowing on soil temperature and soil moisture.

2. Literature Review

2.1 Taxonomy

The only detailed taxonomic and life-history study of western snowberry (*S. occidentalis*) was made by Pelton (1953). Western snowberry, also referred to as buckbrush, wolfberry, badgerbrush and chicken willow, is a member of the family *Caprifoliaceae*. Leaves are opposite and ovate, ranging from 3 to 5 cm in length. The densely clustered white or pink flowers, which are born on the tips of current shoots, are distinguished from others of the genus by a companulate corolla with slightly exserted rather than included style and stamens. The fruit consists of a yellowish white berry-like drupe which is produced in the late summer.

2.2 Reproductive Physiology

A highly developed rhizomatous root system accounts for the clonal growth habit of western snowberry (Pelton 1953). In western snowberry, outward colonization occurs by rhizomes, which are true subterranean stems (Pelton 1953, Bold 1967). In time, a single plant will initiate the outward spread of consecutive rings of new plants. Clonal diameter can range from 1 to 200 m. Although overgrazing may hasten the expansion process, snowberry is able to invade dense, vigorous grassland and eventually suppress the competing sod (Pelton 1953).

Although genetically identical stems within a clone are initially interconnected by rhizomes, the degree of interaction that occurs is unclear. Pelton (1953) stated that new plants may be reproductively mature for several years before functional connections with parent plants are severed. Pelton (1953) suggested that, in time, the physical connections would decay. Young plants are thought to be essentially independent of the parent plant by the end of the first growing season, when a separate root system has developed. Willard (1972) demonstrated that application of silvex[1] to a single plant in pairs of

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[1] 2-(2,4,5 trichlorophenoxy) propionic acid; at one time a commonly used brush control herbicide

interconnected plants (*Symphoricarpos orbiculatus* Moench), did not produce herbicidal injury in the untreated members. Like Pelton (1953), Willard concluded that translocation between clonal individuals was probably not significant after the first year of establishment.

According to Engle (1978), two important consequences of the rhizomatous habit are persistence of the original genetic stock and multiplication of new plants under conditions that may be too severe for seedling establishment. In the case of western snowberry, vegetative buds arising from rhizomes and root crowns also enable the shrub to resprout vigorously after defoliation or decapitation. In the excavation of a 10 year old clone of western snowberry, Pelton (1953) determined that the linear ratio of erect main stems to rhizomes was 1:4.4. Such a ratio emphasizes the preponderance of below ground relative to above ground stem tissue.

Although the success rate for new plants establishing from seed is quite low, the dispersal and propagation of snowberry over long distances likely occurs through transport of seed by birds, mammals or water (Pelton 1953, Wheeler 1976). Each berry-like fruit in the fruiting cluster is composed of two seed-like nutlets. Seed durability tests showed variable but adequate survival of snowberry nutlets passing through the digestive tracts of wild and domestic fowl (Pelton 1953).

Fruit clusters do not abscise in autumn and tend to remain attached to the plant for at least one winter before dropping to the ground. A period of two years may be required to break double dormancy. Germination will not proceed until endocarp breakdown and afterripening are complete. Pelton (1953) reported a feeble establishment of snowberry from seed, with only three of the twenty sites surveyed showing viable seedling establishment. Damping-off fungi and drought were identified as the major causes of mortality. The majority of viable seedlings established on disturbed micro-sites, such as the burrows of small mammals.

2.3 Distribution and Ecology

In Canada, western snowberry occurs from the Great Lakes to the interior of British Columbia (Fig. 1) and extends well into the Northwest Territories (Pelton 1953). *S. occidentalis* is the most abundant species in the Northern Great Plains, and is replaced by *S. albus* (L.) Blake to the north and east of its range (Jones 1940).

Western snowberry may occur in a wide variety of communities and vegetation types, ranging from the shrub layer of deciduous forest to open prairie (Pelton 1953). Soil moisture appears to be the principal environmental factor affecting its distribution (Wheeler 1976), although a wide tolerance with respect to soil texture, pH, organic matter and fertility has been reported (Pelton 1953). In his investigation, Pelton (1953) noted that snowberry did not occur on saline or alkaline sites. Wroe (1971) has described a shrub–grass association in the southern parkland of Alberta, with snowberry canopy cover ranging from dense to sparse. Major associated species included *Festuca scabrella* Torr., *Stipa spartea* Trin. *var. curtiseta* Hitch. and *Rosa woodsii* Lindl. Wroe contended that shrub canopy closure related to clone age, with oldest clones having the densest cover. Western snowberry contributed 45% of the total annual production with a canopy cover of 42%. Annual yield of snowberry ranged from 719 to 1626 kg/ha. Of the eight plant communities described by Wroe (1971), the distribution of snowberry was the least predictable.

In the central portion of the aspen parkland, Wheeler (1976) characterized western snowberry stands as closed or open, the former having a near–continuous canopy, the latter being similar to the dense stand in Wroe's study. Wheeler (1976) reported shrub standing crop values for western snowberry of 410 to 3850 kg/ha, depending on stand type. Like Pelton (1953) and unlike Wroe (1971), Wheeler (1976) concluded that soil moisture was the principal factor affecting distribution of western snowberry. Given the drier, more open nature of the southern parkland study site, evaluation of snow drift patterns (Stoeckeler and Dortignac 1941) and the incidence of rodent burrowing (Pelton 1953) might have helped explain the irregular distribution of western snowberry reported

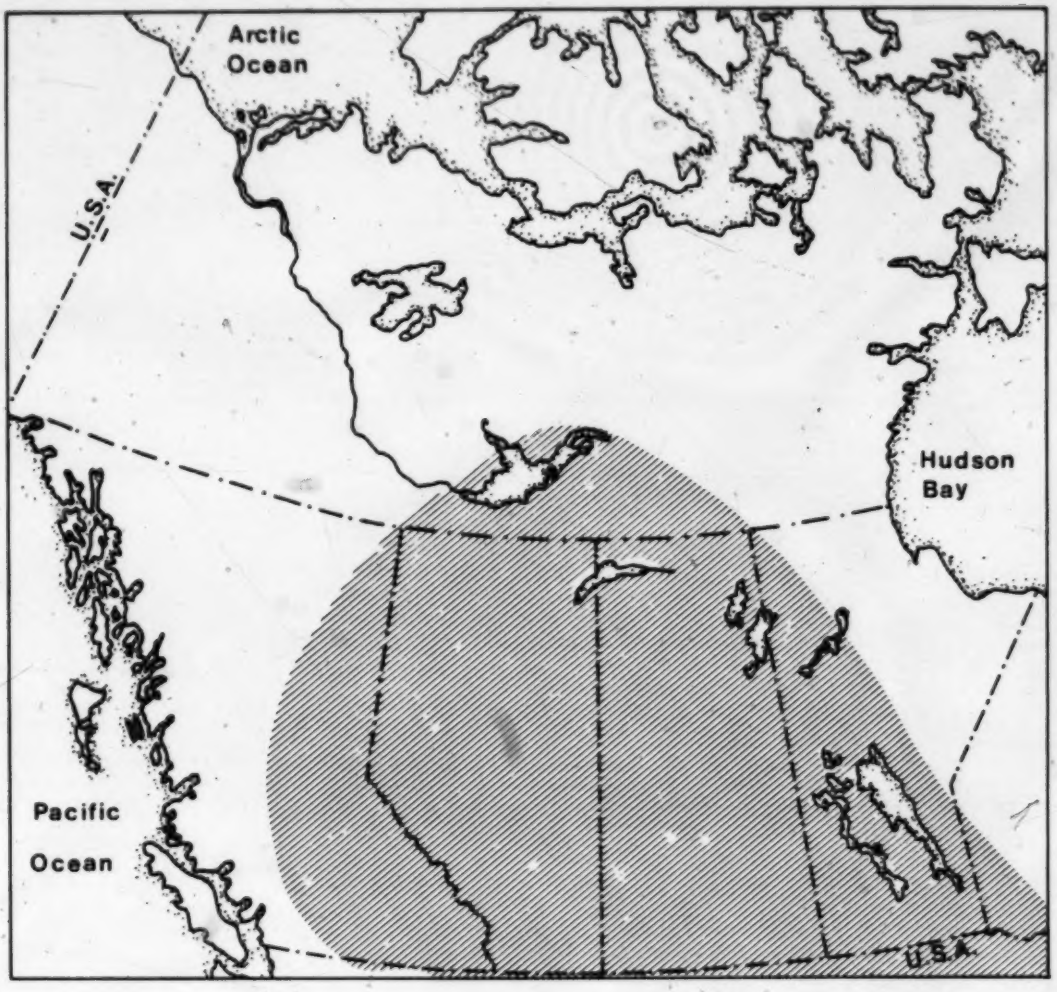

Fig. 1. Distribution of western snowberry in Canada (adapted from Pelton 1953).

by Wroe (1971).

Many authors have speculated that the occurence of western snowberry as an ecotonal shrub, between grassland and woodland, may promote forest succession (Bird 1930, 1961; Pelton 1953; Scheffler 1976; Wheeler 1976). Higher soil temperatures in the shrub relative to the woodland, along with soil moisture levels comparable to the woodland (Scheffler 1976) would likely provide conditions conducive to sucker initiation in aspen poplar (Schier 1976). Although acceptance of such a hypothesis is tempting, further study is required to clearly establish such a role for western snowberry in the ecology of the aspen parkland.

2.4 The Problem of Western Snowberry Encroachment

With the short time requirement for establishment and a tendency to occupy the most productive range sites, western snowberry presents a significant problem in the management of rangeland (Pelton 1953; McCarty 1967). Although historical accounts are limited, Wroe(1971) has described a *S. occidentalis* Hook. -*Festuca scabrella* Torr. association which occupied 8.3% of an ungrazed southern parkland site. Range inventory estimates[2] in the aspen parkland indicate that the aerial extent of western snowberry shrubland on grazed rangeland may be as high as 25% in the southern parkland and up to 40% in the northern fringe.

The accounts of early settlers[3] indicate that the aerial coverage of western snowberry has increased during this century, as has that of other woody species (Bailey and Wroe 1974). The suppression of prairie fires, present versus historical grazing patterns, and climatic cycles, are factors that may explain the present day prominence of western snowberry in the parkland and prairie (Nelson and England 1971). Anderson and Bailey (1980) noted a decline in western snowberry cover where annual burning was practised, suggesting that the incidence of wild fires may figure most prominently in

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[2] Richardson, C.J., Range Management Unit, Public Lands Division, Alberta Energy and Natural Resources. Personal Communication, 1982.
[3] Sharp, R., former employee at Buffalo National Park, Wainwright, Alberta. Personal Communication, 1982.

explaining the change in western snowberry cover.

Like other parkland shrubs (Bailey 1970), western snowberry encroachment reduces the carrying capacity of the range for domestic livestock. With sufficient canopy cover, western snowberry will suppress desirable species, thus reducing forage production. Even with an open canopy type, the shrub presents a physical barrier to domestic grazers. Wroe (1971) reported a 50% reduction in forage production in the southern parkland, while Wheeler (1976) estimated reductions of between 20 and 83%, depending on the degree of shrub canopy closure. In Minnesota, *Poa pratensis* L. was one of the most persistent species under a heavy overstory of western snowberry. Anderson and Bailey (1979) reported a predominance of shade tolerant sedges in dense stands of western snowberry in the aspen parkland.

Most accounts in the literature describe the problems related to western snowberry, when it occurs as a grassland or shrubland species (Pelton 1953, McCarty 1967, Wroe 1971, Wheeler 1976). However, where present as an understory shrub in aspen woodland, the regeneration of western snowberry has plagued attempts to convert such forest to improved pasture (Bailey 1972, FitzGerald 1982). Even where aspen regrowth has been virtually eliminated, snowberry has regenerated vigorously and replaced aspen as the dominant stand component (FitzGerald 1982).

2.5 Control of Western Snowberry

A variety of methods have been tested for control of western snowberry.

2.5.1 Herbicides

Friesen *et al.* (1965) have recommended that for control of western snowberry an application of 2.2 kg/ha of 2,4-D ester, be applied as soon as leaves are fully expanded. Timing of foliar spray applications is important as herbicide penetration into the leaves is thought to decline soon after leaf expansion is complete. Hot and dry weather conditions at the time of application usually result in poor control. Best results

are achieved with ground equipment, where topography permits, since a higher spray volume is possible. Stands up to 0.5 m tall should receive 115 l/ha, while those exceeding this height should receive twice this volume.

Variable results have been reported with 2,4-D. The ester formulation is superior to the amine, with top kills ranging from 46 to 100% and control persisting from 1 to 4 years (Bowes 1966, Corns and Gupta 1966, Skoglund and Coupland 1966, Bailey 1967, McCarty 1967, Switzer and Wroe 1980). The effect of 2,4-D on woody plants is generally limited to the above ground portion (Eliasson and Hallmen 1973). Foliar applied 2,4-D is likely transferred initially by the phloem, but may easily cross over to the xylem stream and be transported acropetally. In western snowberry, once apical dominance is broken, by herbicide injury to the shoot apex, new sprouts may arise from old stems, root crowns or rhizomes. Repeated spraying is therefore required to reduce regrowth potential.

Herbicides have been least effective when western snowberry occurs as an understory shrub in aspen woodland. For example, Bailey (1967) applied 2,4-D ester at 4.5 kg/ha and achieved a first year kill of only 60%. The following year, the reduction in shrub canopy was no longer evident. The low degree of top kill likely resulted from the interception of much of the applied herbicide by the overstory canopy.

Where pure stands of western snowberry have been treated with picloram[4], only minor stand reductions have been achieved, with rates up to 4.5 kg/ha required to provide control for a limited number of years (Bowes 1966, Friesen 1966, Adamson 1967). Switzer and Wroe (1980) reported excellent control of western snowberry, aspen, rose and willow in containment spraying of poplar bluffs (i.e. to prevent further expansion of woodland groves) with 0.5 kg/ha of picloram and 2 kg/ha of 2,4-D ester. This combination of herbicides gave 2 to 3 years of control, while the straight 2,4-D ester treatment showed no visible reduction 2 years after treatment. Picloram tends to bind with soil colloids, especially organic matter (Grover 1972). If soil activity is, in fact,

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[4]4-amino-3,5,6-trichloropicolinic acid.

important in the mode of action of this herbicide, soil type may be an important factor explaining the variation in kill reported.

Foliar sprays of DPX-T6376-21[5] at 0.12 to 1.0 kg/ha (Standish and Blackshaw 1981, Bowes 1982) and HOE 39866[6] at 1.75 to 3.5 kg/ha (McIver et al. 1981, Bowes 1982) have given excellent one season control on western snowberry, although injury to native grasses may be excessive (Bowes 1982). Roller drum applications of glyphosate[7] during late summer also show promise (Friesen and O'Sullivan 1979).

With a mow-spray (2,4-D ester) combination, Corns and Cole (1973) achieved one of the best levels of control reported in the literature. In their study, the regrowth of western snowberry that arose after mowing on June 10, was sprayed on July 29. Although the initial kill and increase in forage production was impressive, resprouting was well underway by the third season after treatment.

2.5.2 Burning

Western snowberry is highly adapted to periodic burning (Pelton 1953). Anderson and Bailey (1979) reported that three months after a spring burn, western snowberry had re-established a canopy cover equivalent to that of unburned stands. Initially, stem density in the burned stands increased by 3 to 5 times compared to the unburned, but then declined in the second and third years after treatment. Although a single spring burn altered stand structure by producing more and smaller stems, snowberry quickly regained dominance over the shade tolerant sedges and forbs that were present.

Annual burning of western snowberry shrubland had a more pronounced effect on the shrub (Anderson and Bailey 1980). On rangeland burned annually in early spring for 25 years, snowberry cover declined from 31% in the unburned to 2% in the burned. However, frequency remained unchanged at 52%.

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[5]Methyl 2-[[[[(4-Methoxy-6-Methyl-1,3,5-triazin-2-yl) amino]carbonyl]amino]sulfonyl]benzoate.
[6]Hoechst Canada Inc.
[7]N-(phosphonomethyl) glycine

Other members of the genus appear less adapted to fire. Aldous (1934) and Launchbaugh and Owensby (1978) have reported that *S. orbiculatus* Moench. could be eliminated with annual late spring burning carried out 2 to 3 years in succession, in the tall grass prairie of Kansas.

2.5.3 Grazing and Mowing

FitzGerald (1982) found that a single spring burn of aspen forest, followed by heavy grazing by cattle, either early or late in the season, produced two very different plant communities. Regrowth following spring grazing was predominantly of aspen suckers and herbage. In the late grazing treatment, western snowberry and herbage formed the major biomass components. Early season defoliation should result in the greatest level of control, probably because spring tends to be the time when plant NSC reserves are depleted (Launchbaugh and Owensby 1978). Contrary to this, FitzGerald found that the late-season grazing treatment dramatically reduced aspen poplar as a stand component. It was postulated that late grazing interrupted the normal induction of dormancy and frost hardening in aspen and, hence, left overwintering organs (i.e., root crowns and roots) vulnerable to frost damage. Substantial aspen control, after a single spring burn and late grazing, is significant, considering the massive volume of literature documenting the regenerative potential of aspen (Berry and Stiell 1978, Perala 1979, Schier 1981).

Might late season defoliation have value in the control of snowberry? Western snowberry increased under late grazing in FitzGerald's study, but snowberry was only lightly defoliated by the grazing cattle. Because of the low palatability of snowberry to cattle, complete defoliation was not possible through grazing, even though preference for the shrub increased in the late summer. If removal of all leaf area is required to cause winter injury (Fuchigami *et al*. 1971), snowberry may have retained sufficient foliage for the normal induction of dormancy to occur.

Accounts of the effect of mechanical defoliation on western snowberry are sketchy. Pelton (1953) found that, in Minnesota, season of defoliation and soil moisture regime influenced the regeneration of the shrub. Working with limited plant numbers on dry and moist sites, resprouting in late summer occurred only if decapitation took place prior to normal bud dormancy. The degree of stand regeneration during the following season differed with moisture regime and season of cutting. The greatest reduction was associated with an early August cut where soil moisture conditions were characterized as dry. Similarly, Corns and Cole (1973) reported that a July 29 mowing gave the greatest initial reduction in plant numbers when compared with a June 10 single cut or cutting on both dates. Although treatment effect was short-lived with late cutting, plant numbers the season after cutting, were reduced by 50%.

2.6 Factors Affecting Regeneration of Woody Species

A variety of factors influence sprouting and regeneration following defoliation.

2.6.1 Vegetative Buds

Upon release from apical dominance, new shoots will elongate from vegetative buds. Vegetative buds differ in their mode of origin, developmental status and abundance (Table 1).

Vegetative buds may be categorized as either "axillary" or "adventitious", based on their mode of origin (Kramer and Kozlowski 1979). The former bud type develops in axillary positions, initially with subtending leaves, but in mature plants, they may range in position from the stump base to the upper branches. Axillary buds originate from meristematic tissues having preformed vascular connections (Garrison 1952, Kozlowski 1971a). Axillary buds may persist for the life of the woody plant (Kozlowski 1971a). In contrast, adventitious buds develop on roots from meristems that arise during root growth, after the formation of the phellogen or cork cambium. They are further distinguished from axillary buds by the lack of a preformed vascular connection to the pith (MacDaniels 1953, Esau 1965, Schier 1976).

All vegetative buds start off as primordia which may range in size from microscopic to that of a small protuberance 1 to 2 mm in diameter. A more advanced developmental state is referred to by Schier (1973a) as a "suppressed" bud (Table 1). In this state, buds are clearly visible and have bud scales. Adventitious buds will have acquired vascular connections by this point. Given the necessary stimuli, suppressed buds will elongate into shoots.

In aspen poplar, defoliation stimulates the development of primordia to the suppressed bud state (Schier 1973a). For woody plants in general, most reports indicate that following severe defoliation or decapitation, axillary buds located at the stump base are the first to release and elongate into new shoots (Stone and Stone 1943, McDaniels 1953). With repeated defoliation, each subsequent wave of sprouts will tend to arise

Table 1. Definitions describing types of vegetative buds in woody plants.

Bud Type	Definition	Reference
1. Axillary	Describes buds arising from meristematic tissues which have preformed vascular connections. They are usually first visible in the leaf axils of juvenile plants but in older plants may be found from the stump base to the stem apex.	Garrison 1971 Kozlowski 1971a
2. Adventitious	Describes buds arising from the phellogen or cork cambium of roots and sometimes stems of woody plants. Adventitious buds do not have preformed vascular connections and must develop these before they can elongate into shoots.	MacDaniels 1953 Esau 1965 Schier 1976
3. Suppressed	Describes buds which are sufficiently advanced, anatomically, to elongate into shoots, but are held in a quiescent state, likely by hormonal inhibition.	Schier 1981
4. Currently initiated	Buds which may differentiate from pre-existing primordia and then elongate into new shoots, during the season of disturbance to the parent plant. Though there may be other buds present which are developmentally more advanced, currently initiated buds may provide the major source of new shoots after a disturbance.	Schier 1981

from "currently initiated" buds. These are "axillary" buds which differentiate in close proximity to the bases of shoots which were released after the initial defoliation (Schier 1973a). The supply of axillary buds will be temporarily depleted after the initial cut, but sprouts released with subsequent cuts, will arise from currently initiated axillary buds (Schier 1981). In this way, an ample supply of vegetative buds, of advanced developmental status, remain in reserve. Axillary and currently initiated (axillary) buds provide the principal source of new shoots, and adventitious buds release only in conjunction with abnormal environmental stimuli or after injury or depletion of the primary supply (Kramer and Kozlowski 1979)

The tendency for axillary buds to release prior to adventitious ones seems clearly related to their more advanced developmental status (Sandberg 1951, Schier 1973a). Owing to the lack of direct vascular connections, adventitious buds may not respond to hormonal stimuli or obtain growth substances as readily as axillary buds. Furthermore, a greater supply of carbohydrate may be required for their release as new shoots. Thorpe and Murashige (1970) observed a heavy accumulation of starch in association with shoot primordia differentiating in tobacco callus culture. They concluded that this starch accumulation was indicative of the high energy cost of the process. Since adventitious buds must undergo more developmental changes to reach the "suppressed" bud state, a higher energy expenditure would be expected.

2.6.2 Hormonal Control

Phillips (1975) discussed several current theories explaining apical dominance and the release of vegetative buds following removal of the shoot apex. A hormonal balance theory, which stresses the interaction of auxin and cytokinin, is currently favoured. Auxins produced in the apical meristem are subject to basipetal transport which is required to offset a continuous process of auxin inactivation (Eliasson 1971a, 1972). This constant downward supply inhibits the initiation and elongation of shoots (Eliasson 1961, Farmer 1962). Top removal will cut off the downward flow of auxin, thus reducing

inhibitory concentrations of the hormone in crown and root regions and thus releasing suppressed shoot primordia (Schier 1976).

Cytokinins are produced in actively growing root tips and are transported upward in the xylem stream (Forsyth and Van Staden, 1981). Acting independently of auxins, cytokinins stimulate both the initiation of primordia and the release of suppressed buds (Peterson, 1975). With top removal, the concentration of cytokinins temporarily increases in the roots due to the elimination of upward translocation. The increase in cytokinin relative to auxin facilitates bud release (Schier 1979).

Auxins may, in fact, maintain apical dominance by promoting the degradation of cytokinins (Schier 1981). Consequently, cytokinins may only exert their stimulative role when the auxin to cytokinin ratio declines beyond a certain level.

Other hormonal factors may influence bud initiation or emergence subsequent to defoliation. For example, abscisic acid (ABA), a dormancy-promoting hormone, may prevent bud release if defoliation takes place after the onset of dormancy. This response may relate to the accumulation of ABA in vegetative buds because of a decline in the late-season translocation and metabolism of the hormone (Phillips and Hoffman 1979). Dorffling (1964, 1966) demonstrated the inhibition of bud outgrowth in decapitated seedlings of *Acer pseudoplatanus* L. and *Pisum sativum* L. with application of inhibitor extracts of the same species. The eventual release of *Acer saccharum* Marsh. buds would not occur until endogenous levels of cytokinin increased to counter the inhibitory levels of ABA (Taylor and Dumbroff 1974). In *Acer pseudoplatanus* L., bud emergence from dormancy may have been related to increases in endogenous gibberellic acid levels (Phillips and Hoffman, 1979).

Aside from the hormonal factors that control bud release, shoot outgrowth may be regulated by seasonal variation in growth promoters and inhibitors. Seasonal variation in endogenous levels of auxin, cytokinin and abscisic acid in woody plants, has been documented (Hatcher 1959, Luckwill and Whyte 1968, Seeley and Powell 1981). This seasonal variation may partially explain the "episodic" character of growth (Doorenbos

1953). Tinklin and Schwabe (1970) found that defoliation at progressively later dates in the growing season, resulted in a reduced growth response at each subsequent date.

2.6.3 Carbohydrate Reserves

Much of the research relating to regeneration following defoliation has emphasized the role of reserve supplies of nonstructural carbohydrates or NSC (Berg and Plumb 1972). Compounds such as glucose, fructose, fructosans, dextrins and starch are mobilizable and can be manipulated to fuel plant growth and development (Smith 1969). Garrison (1971) pointed out that each genus has its own seasonal reserve curve, as determined by the interaction between the genetic make up of each plant species and the unique environment in which it resides. A predictable annual cycle in NSC reserve levels results from the balance between respiration, new leaf and twig production and fruit formation, which reduce reserve levels, and photosynthetic activity, which replenishes these reserves (Berg and Plumb 1972).

Sprouting woody plants depend on NSC for vegetative regeneration after top removal. Schier and Zasada (1973) found that resultant stem density and aerial biomass in aspen clones were correlated with NSC levels at the time of cutting. They further concluded that aspen depended on NSC until new shoots broke the surface and established new leaf area. In *Populus deltoides* Marsh. (Larsen and Dicksen 1973) and *Malus spp.* (Hansen 1971), dependence on reserve NSC persisted to the 8 and 5 leaf stages, respectively. Although dependence on reserves may decline fairly soon after emergence, replenishment of root reserves may not take place until quite late in the season (Kozlowski and Keller 1966).

The total pool of carboyhydrate reserves available for regrowth depends on the timing of cutting or defoliation relative to the annual NSC reserve cycle (Butterly *et al.* 1959, Jones and Laude 1960). The seasonal low in NSC for most shrubs occurs in spring towards the end of leaf flush, and again during flowering and fruit production (Jones and Laude 1960). This pattern has been confirmed for *Symphoricarpos oreophilus* Gray and

S. vaccinoides Rydb.(Donart 1969, Willard and McKell 1978), and is expected to be similar in *S. occidentalis* Hook. (Pelton 1953).

Timing of defoliation will influence the length of growing season available for the production of new growth and the replenishment of NSC reserves. Donart and Cook (1970) clipped 90% of the shoots from the previous season on *S. vaccinoides* Rydb. and determined that lost reserves were recovered when 20% of the regrowth had been produced. In horticultural crops, late-season pruning, fertilization or excessive irrigation may induce late season growth, reducing food reserves and leaving little time for replenishment of reserves (Berg and Plumb 1972).

Schier (1976) pointed out that there are finite limits to the frequency of defoliation that sprouting woody plants can withstand. Repeated burning, mowing, grazing or herbicide application will deplete carbohydrate reserves and reduce the potential for vegetative regeneration. Berry and Stiel (1978) determined that aspen regrowth progressively declined with harvest rotations of less than once every ten years. They attributed the reduction in regrowth potential to "being starved of adequate feedback from photosynthesizing tops". Six defoliations of *Symphoricarpos oreophilus* Gray, over two years, resulted in NSC depletion and plant mortality by the second season (George and McKell 1978a). High stem mortality during the dormant period was attributed to low levels of NSC.

2.6.4 Winter Hardiness

Season of defoliation may affect the induction of dormancy in temperate woody plants. Fuchigami *et al*. (1971) demonstrated that defoliation of *Cornus stolonifera* Michx., during short day conditions, limited the level of frost hardiness that could develop. When compared to untreated plants, tissue injury in defoliated plants was observed in the −5 to −10°C range. They hypothesized that timely defoliation in the treated plants may have interrupted the translocation of a hardiness promoting factor(s) produced in the leaves under short days.

Carbohydrate reserves also affect the development of winter hardiness (Levitt 1980, Siminovitch 1981). NSC acts as a cryoprotectant, and, as an energy source for membrane-protoplasm augmentation and for various metabolic processes unique to the development of winter hardiness (Siminovitch 1981). Reduction of fall NSC levels by defoliation, girdling or disease have all been reported to limit the development of winter hardiness (Siminovitch 1981). Even if the reduction is insufficient to kill the plant, sublethal winter stress may reduce yields in subsequent growing seasons (McKenzie and McLean 1980a).

As was the case for late season recharge of NSC, horticultural practice has acknowledged, for at least 100 years, the potential for late season pruning to cause winter injury (Roe 1881, Auchter and Knapp 1929).

2.6.5 Environmental Factors

Variation in climatic factors may also affect the release of vegetative buds (Schier 1976). Bailey and Wroe (1974) reported greater aspen sucker establishment with higher air temperatures one and two years prior to establishment. They found precipitation two years prior to be negatively correlated. High ambient temperatures or low soil moisture levels, that reduce apical growth, may explain the release of vegetative buds. Such conditions may result in reduced auxin production and hence basipetal flow of the hormone. A change in the ratio of auxin to cytokinin would result, allowing the initiation and/or release of vegetative buds.

The precise role of soil temperature in the release of vegetative buds, in an undisturbed environment, remains controversial. Higher soil temperatures may enhance the degradation of auxin (Schier 1976). However, Steneker (1974) has reported that the reduction in auxin relative to cytokinin may be insufficient to break apical dominance. Nonetheless, where disturbance occurs, higher soil temperatures have been associated with a greater sprouting response (Schier 1976, Schier and Campbell 1978).

Environmental conditions affecting the rate and duration of regrowth may also affect the actual level to which NSC reserves are reduced. Wenger (1953) demonstrated that depletion of NSC following cutting of *Liquidambar styraciflua* was proportional to new growth produced. Environmental conditions which favour vegetative growth, especially available soil moisture and fertility, will also favour NSC depletion (Berg and Plumb 1972).

Drought conditions following the onset of regeneration may limit replenishment of NSC reserves (Willard 1972). However, drought at the time of defoliation may impose an enforced dormancy such that both regrowth and NSC draw-down may be delayed until moisture availability improves.

2.6.6 Clonal and Site Variation

Factors such as genotype, clonal history, clonal age and site variation may account for differences in regenerative response. Pelton (1953) determined that in western snowberry, clone diameter increased with age, and stem height increased with soil moisture level. He noted other clonal differences in leaf shape and stem density but could only speculate as to the source of this variation. Schier (1976) reported clonal variation in aspen sucker initiation and development in response to defoliation. Differences in the clonal factors listed above may contribute to variation in the developmental status of vegetative buds, and thus the regenerative potential of individual clones. Although genotype likely contributes to differences in regenerative response, most differences have been related to nongenotypic factors (Schier 1981). For example, aspen clones with a history of fire, grazing or mechanical disturbance may have a greater regenerative potential than undisturbed clones (Schier 1973). On sites where aspen is shallow-rooted, regenerative potential may be reduced where fire may damage vegetative buds on root crowns and rhizomes (Schier and Campbell 1978).

3. Methods and Materials

3.1 Experimental Sites

3.1.1 Beaverhill Lake

The principal field study area was located on a grazing lease administered by the Alberta Public Lands Division of the Department of Energy and Natural Resources. This site is in central Alberta (Fig. 2), near the south-eastern shore of Beaverhill Lake (elevation 670 meters; approximate latitude 53 23'N). Wonders (1969) has described the climate of the area as "dry subhumid" implying cold winters and mild, dry summers. Annual precipitation averages 576 mm, of which 64% falls during the growing season[1]. The frost free growing period generally ranges from 100 to 120 days in this portion of central Alberta, with the first killing frost usually occurring during the first two weeks of September.

Soils on the experimental site were developed on stratified lacustrine materials overlying glacial till. Soils are intermediate in development between those of purely lacustrine or till plain origin. Ehlert (1981) and Howitt (1981) have mapped these soils as thin, gleyed black chernozems. Core sampling, carrried out by the author, revealed a thin layer of fine textured sand overlying lacustrine clay. Abundant orange and blue mottles in the C horizon confirmed the variable and generally imperfect drainage conditions associated with the profile classification reported above. Site productivity would be expected to be high given the ample moisture supply of the subsoil combined with the chernozemic properties of the surface horizon.

Western snowberry cover occupied 60-70% of the experimental area. In the interspersed grassland, dominant species included *Poa pratensis* L., *Agropyron subsecundum* (Link.)Hitch., *A. trachycaulum* (Link.)Hitch., *Achillea millefolium* L. and *Grindelia squarrosa* (Pursh.)Dunal. Within shrub stands, understory species composition

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[1]Data abstracted from the Tofield North weather station, located 22 km northwest of the experimental site, for 1974-1980

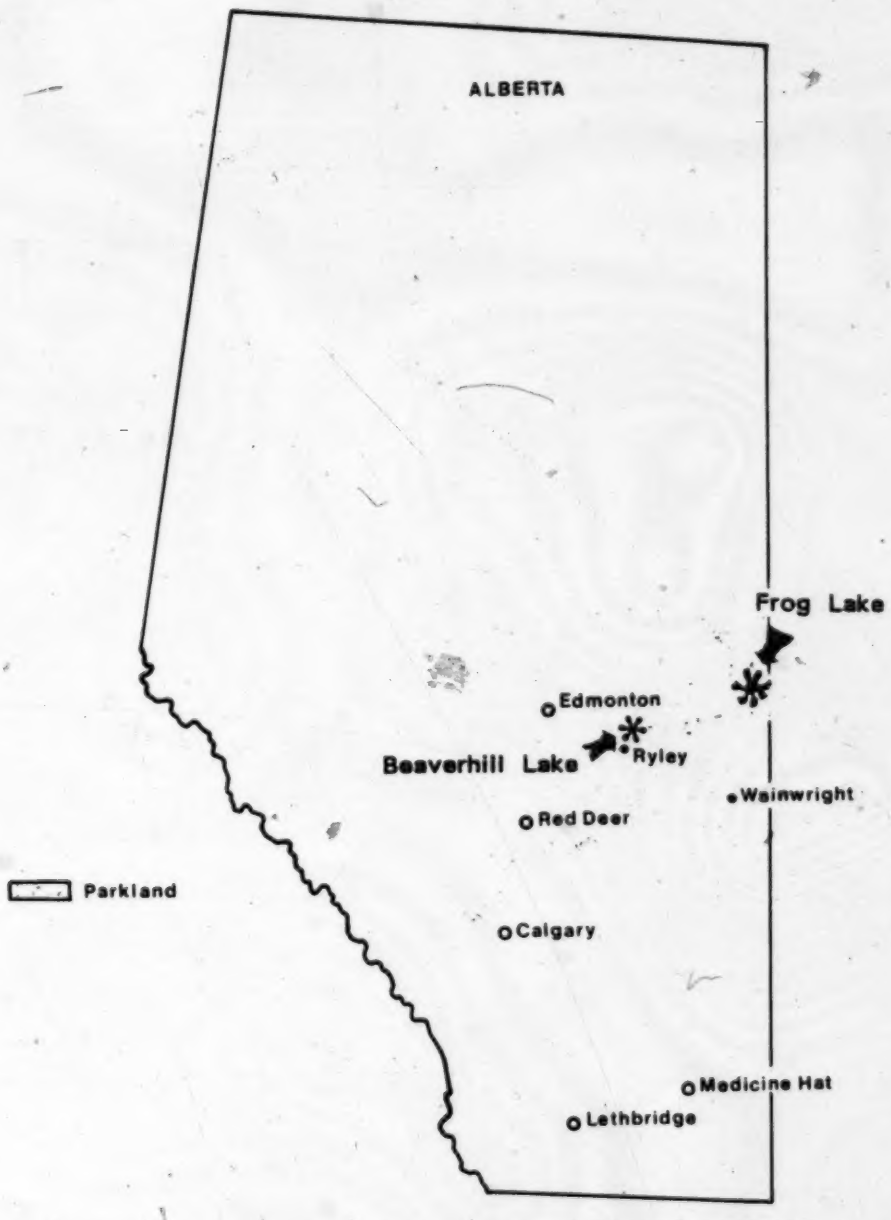

Fig. 2. Location of the Beaverhill Lake and Frog Lake field study areas in east Central Alberta (adapted from Sinton 1980).

was very simple. *Poa pratensis* was most abundant with minor components including *Galium boreale* L., *Cirsium arvense* (L.)Scop. and *Lactuca pulchella* (Pursh.)DC.

3.1.2 Frog Lake

A secondary study site was located on crown land in east central Alberta, near Frog Lake (S.E. 23, Twp. 55, Rge. 3, W 4M; Fig.2). Although general climatic conditions are comparable between the two sites in question (Wonders 1969), the Frog Lake site was characterized by much drier site conditions. Whereas gleyed black chernozems predominated at the Beaverhill Lake site, at Frog Lake, orthic black chernozems were developed on ablation moraine with rolling to "knob and kettle" topography. The experimental site was on the midslope of an east-facing ridge.

3.2 Experimental Design and Treatments

3.2.1 Beaverhill Lake – Main Study

Pelton (1953) and Willard (1972) defined a single plant unit within a snowberry clone, as an enlarged rhizome section with a distinct cluster of stems, and including the immediate roots. Within a snowberry clone, interplant translocation was considered unlikely, but their results were inconclusive in this regard. To eliminate any possible problems that could arise where more than one mowing treatment might be applied within the confines of a snowberry colony, individual clones were selected as the experimental plot units.

A 4-ha site (Fig. 3) was fenced and a population of treatment clones was identified during August 1980. The Beaverhill Lake location was selected because 50 to 60 distinquishable clones of western snowberry were present on level terrain. All clones were visually rated for canopy density, height and diameter. Selection of clones for the treatment population favoured those of dense canopy (90-100% cover), height of 0.7 to 1 m and diameter ranging from 15 to 25 m. Because there were no obvious criteria for

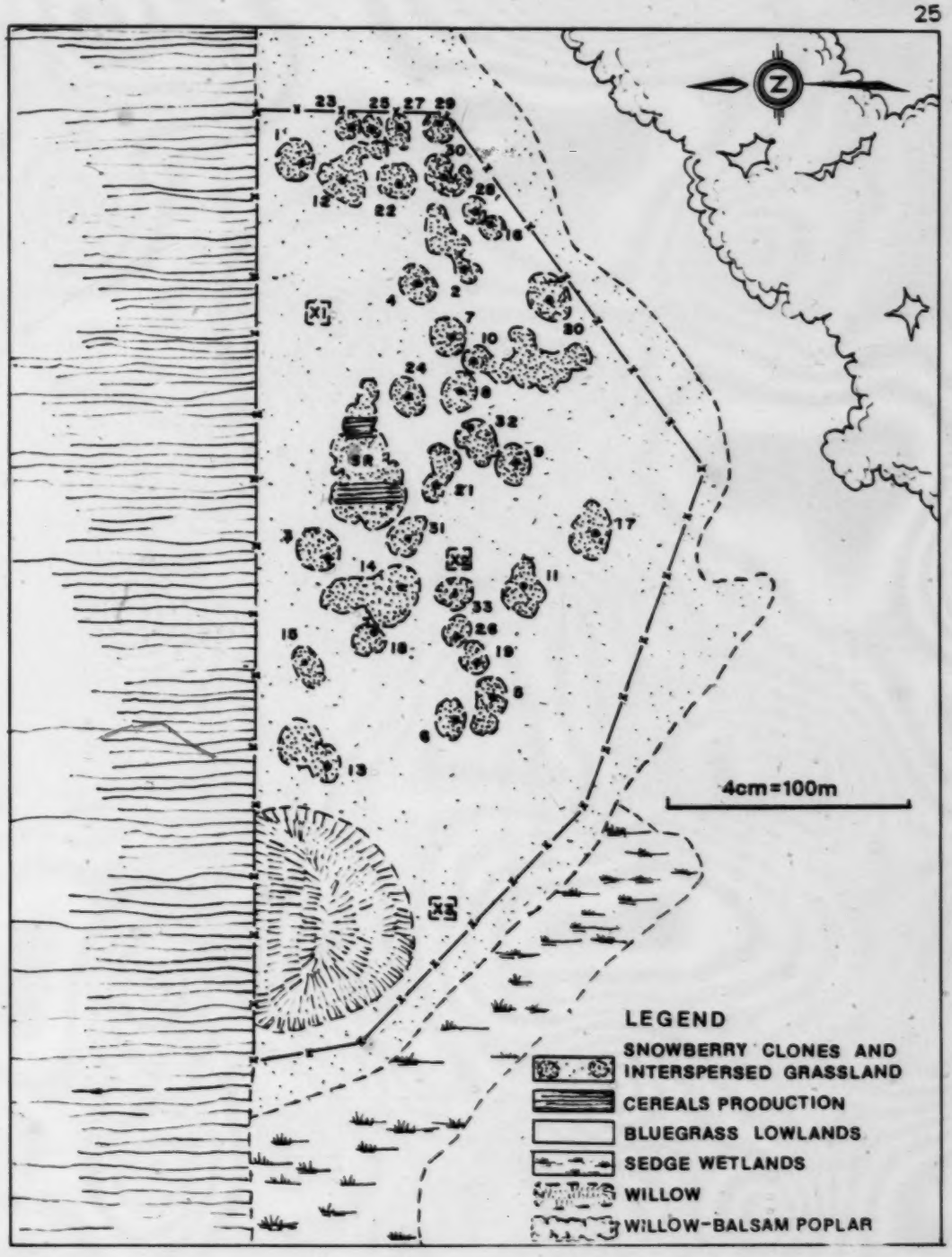

Fig. 3. Site plan for the Beaverhill Lake study (N.E. 16, Twp. 52, Rge. 17, W4M). Treatment clones are individually numbered (1-32), [X1] weather station, [X2] micrologger location and hydrogen probe-set 1, [X3] hydrogen probe-set 2, SR strip mowing plots.

subdivision of treatment clones into blocks, a completely randomized design was employed.

Eight mowing treatments, consisting of a control plus all possible combinations of single, double and triple cuts on three dates, were applied (Table 2). Cutting dates were selected to coincide with morphologically distinct phenological events:

a. Spring – leaf emergence

b. Summer – flower bud swelling, and

c. Late summer – fruit swelling.

In 1981, treatment dates were May 8, June 24 and August 13, hereafter referred to as spring, summer and late-summer. The spring and summer dates were timed to coincide with expected lows in the NSC cycle, and the late summer date with the onset of dormancy. Four replicates of each of the eight treatments were randomly allocated to 32 clones from the pre-selected population.

Clone mowing was accomplished in two stages, initially with a gyro mower[9], and later with a lawn mower. Stem stubble height averaged 10 to 15 cm after the gyro mowing, with a few plant tops remaining only partially severed. The second cut with the lawn mower left an even stump height (5 to 7 cm), and insured that all tops were cleanly severed. After each mowing, ten permanent sampling stations were randomly located in each clone and marked by a wooden stake. These points were used to make periodic measurements of sprout growth and development.

3.2.2 Beaverhill Lake – Dormancy Response

The late-summer cutting date was expected to coincide with the onset of dormancy. To provide additional information on the timing of dormancy and the dormancy response to defoliation, two additional clones (Fig. 3) were surveyed into a sequence of

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[9]Paulk, 3 point hitch mounted, 1.2 m cutting diameter.

Table 2. Season and frequency of mowing by treatment as applied in 1981 at Beaverhill Lake

Treatments	Spring[1]	Summer[2]	Late Summer[3]
	May 8	June 24	August 13
A	Control	(Unmowed)	
B	X		
C		X	
D			X
E	X	X	
F		X	X
G	X		X
H	X	X	X

[1]May 8 to June 24 = 47 days
[2]June 24 to August 13 = 50 days
[3]August 13 to leaf senesence = 20 days

five strips (2 x 10 m) and were marked with wooden stakes. Randomly selected strips were then mowed at seven day intervals commencing August 7, 1981. In 1982, the procedure was repeated on previously unmowed extensions of the same strips for the same dates.

3.2.3 Frog Lake – Pilot Study

A rectangular section of a snowberry clone was fenced in the spring of 1979, prior to the commencement of the present study. The fenced area was subdivided into three plots, each 5 x 5 m in size. One plot was mowed on July 29, 1979, a second on April 27, 1982 and the third remained as a control. The mowed plots were cut to a 5 cm stubble with a lawn mower. Root connections were severed between the three plots with a profile spade.

3.3 Environmental Measurements

3.3.1 Daily Air Temperature and Precipitation

A standard weather station was established and maintained at the Beaverhill Lake site for the duration of the study. A thermograph (Kahlsico, El Cajon, Calif.), housed in a Stevenson screen, recorded ambient temperature continuously. Daily maximum and minimum temperatures were abstracted from the drum trace for each recording period. Each monthly data set was then standardized with maximum and minimum thermometer readings to correct for error in machine calibration.

A Universal recording rain gauge (Belfort, Baltimore), monitored the daily occurrence and approximate amount (mm) of precipitation. Total monthly accumulations, measured with a Type B rain gauge (Belfort, Baltimore), were used to standardize the daily increments. Weather records from the station on the experimental site were compared with those of the Tofield North station. Monthly means for air temperature and precipitation values were within 5 to 10% of those for the Tofield North station.

3.3.2 Summer Soil Temperature and Soil Moisture

3.3.2.1 1981

In 1981, soil temperature was recorded at 4 to 10 day intervals from March 24 to August 15. Temperature was monitored at 5 and 10 cm depths in interspersed grassland, shrub, single mowed shrub and double mowed shrub cover types. Temperature was measured with a 15 cm soil probe type thermometer.[10] Soil temperature was consistently measured in the early afternoon between 12 noon and 2 pm. Four cover types were sequentially sampled (at two depths) for a total of five readings per type. Temperature readings were adjusted because of thermometer error. The necessary correction factor was derived by water bath calibration.

Gravimetric determination of soil moisture was made on five dates in 1981 (April 27, June 11, July 16, August 12 and September 12). On each date, 15 sample

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[10]Reotemp model J-210, Fisher Scientific, Edmonton.

cores of the surface 15 cm were collected in each of the 32 control and treatment clones and were then bulked together on a clonal basis. Moist soil samples were sealed in air-tight bags and returned to the laboratory. Samples of moist soil were weighed, dried at 100°C until a stable weight was reached, and then reweighed. Soil moisture was expressed on a percent dry weight basis.

3.3.2.2 1982

During the second field season, thermistors[11] were inserted beneath shrub and late-mowed cover types (2 thermistors under each type). Weekly readings were made with a Tele-Thermometer[12] by sequentially connecting each thermistor jack. Readings could be made at all stations within a 10 to 15 minute period thus reducing sampling error caused by variable cloud cover and wind speed.

Soil moisture levels were monitored under shrub and fall mowed shrub cover types with a neutron probe.[13] Two sampling stations were selected; they spanned the slight variation in site relief (Fig. 3). At each of the two sites, sampling tubes were located in pairs, one in a shrub type the other in a late mowed shrub treatment. Sample holes were augered and tubing was seated to a depth of 70 cm, on May 1, 1982. Sampling depths were set for 10 to 25, 30 to 45 and 50 to 65 cm using blocks attached to the neutron probe cable. Since solar radiation may influence surface readings, the first sampling level was at the 10 to 25 cm depth. Weekly readings were made in the four sampling tubes in conjunction with other plot measurements. Three standard curves, one for each horizon, were developed for each of the two sample sites by plotting gravimetric values with probe ratios. Auger samples, from which the gravimetric values were determined, were gathered on June 28, July 26 and August 26.

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[11]Series 400 probe, Y.S. Instruments, Yellow Springs, Ohio.
[12]Model 425C with +.1°C precision, Y.S. Instruments, Yellow Springs, Ohio.
[13]Hydrogen Probe, Model 503, Campbell Pacific Nuclear, Pacheco, Calif.

3.3.3 Winter Soil Temperature and Snow Depth

During the winter of 1981-82, a continuously recording weather station[14] monitored soil temperature at 5 cm under shrub and late-mowed shrub cover types. The plots to be monitored were adjacent to one another, with their intersection lying parallel to the prevailing wind. A thermistor was inserted into each cover type, and the recorder was housed in an insulated box.

Snow depth over each thermistor, was measured from calibrated stakes placed on site in late November. Disturbance was eliminated within a 3 to 4 m radius of the sampling points.

3.3.4 Site Variation Among Snowberry Clones

Although there were no obvious site differences between snowberry clones, measurements of depth of sand and distance to wetland cover types (sedge and willow) were made to help account for any variation among clones with respect to treatment effect. Two auger holes were excavated in each clone and the depth of sand was recorded. Distance to wetland cover was estimated from Fig. 3. Clone locations were plotted from azimuth, and distance measurements were made progressively from a tiepoint (i.e. N.E. corner of the fenced site) to each clone centre.

3.4 Nonstructural Carbohydrate and Sprouting Reserve Studies

3.4.1 Field Sampling

3.4.1.1 Seasonal Variation in Nonstructural Carbohydrate

Nonstructural carbohydrate levels were determined for control and single spring mowed treatments on 12 dates in 1981, from April 15 to October 16. The sampling interval averaged 10 days in the spring and early summer and 15 days towards autumn. On each sampling date, two "plants" were randomly chosen from the four clones of each treatment. A cylinder of soil, 30 cm in diameter and 30 cm

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[14]CR21-Micrologger, Campbell Scientific Ltd., Logan, Utah.

deep, was excavated around each plant. Old stem, root crown, large roots (>3 mm diameter) and small roots (<3 mm) were collected from the control clones, while only the root crown was sampled in spring mowed clones.

Plants of intermediate age were selected, with clone centres and edges being avoided. Samples were separated by tissue type and placed on dry ice within 15 to 30 minutes of excavation, returned to the laboratory, and stored in a −10°C freezer until further processing could be carried out.

3.4.1.2 Effect of Treatment on Fall Sprouting Reserves

Using the sampling procedures outlined above, root crown samples were collected from all control and treatment clones on two dates. On April 15, 1981, prior to any visible signs of growth, two root crowns were collected from each of the 32 clones, and were stored for NSC determination. On October 27, 1981, three root crowns were collected from each clone, for NSC and etiolated growth (EG) determination. Etiolated growth was employed as a measure of regrowth potential, based on the dry weight of shoots grown out in the dark, from root crowns of western snowberry. Proximal and distal portions of each root crown sample were clipped off and transferred to cold storage; middle sections were tagged, placed on moist vermiculite and returned to the laboratory.

3.4.2 Carbohydrate analysis

Total nonstructural carbohydrates (NSC) were extracted from snowberry tissues using the enzyme digestion technique outlined by Smith (1969). The frozen field samples were freeze-dried until a constant weight was reached[15]. This procedure required 3 to 4 days in the drier. The freeze dried samples were crushed into small pieces, with care being taken to remove discolored tissues indicative of injury or stem mortality. Tissues were ground in a Wiley mill to pass a 40 mesh screen. After thorough mixing of the total ground volume, a 2.5 g subsample was placed in a tightly sealed 10 ml vial. The small-root fraction (<3 mm diameter) was not analysed due to excessive variation in sample color and

[15]Freeze drier – Virtis, model 50 SRC – Gardiner N.Y., U.S.A.

quantity. Analysis of the spring sampling of all clones and the seasonal NSC samples was carried out by Cantest Laboratories of Vancouver, B.C. Samples from the October collection were processed by the author.

From a sample of 350 mg of ground tissue, disaccharides and starch were hydrolysed with 0.5% alpha-amylase[16] solution for 48 hours at pH 4.45 and 38°C. Fructosan breakdown was insured by 0.1 N sulfuric acid. The Schaeffer-Somogyi copper-iodometric titration method, as outlined by Smith (1969) was used to assay for reducing sugars.

Prior to the NSC analysis carried out by the author, the pH and temperature recommendations of Sigma Chemical Co. and Smith (1969) were compared for their effect on yield of reducing sugars[17] Two pH and temperature regimes were tested with three samples of each of three tissue lots. The only significant effect on yield of reducing sugars was due to pH. The pH of 4.45 recommended by Smith (1969) gave a significantly higher yield, while temperature showed no significant effect[18]. The more acid pH level was thought to enhance the hydrolysis process. In both the analysis by Cantest Ltd. and that carried out by the author, the conditions of Smith (1969) were employed. Final NSC analysis results were expressed on a percent dry weight basis.

3.4.3 Etiolated Growth Determination

Immediately following field sampling, root crowns were prepared for expression of etiolated growth (EG) in the dark chamber following the procedure outlined by FitzGerald (1982). After fresh weights were determined, the samples were soaked for five minutes in a fungicide solution[19] to reduce pathogen activity. Cut ends were sealed with molten paraffin. Treated crowns were placed in a dark growth chamber. Temperatures of 25/15°C were maintained for a 16/8 hour day/night cycle, with constant relative humidity set at 70%. Trays were watered every 1 to 2 days and a green safelight

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[16]Enzyme Commision Number 3.2.1.1, 1,4-alpha-D-Glucanohydrolase, produced by SIGMA Chemical Co., St. Louis, Mo.
[17]The Sigma bottle label specified a specific enzyme activity at pH 6.9 and 22°C while Smith (1969) designated a pH of 4.45 and temperature of 38°C.
[18]Analysis of variance of results in Appendix 1-A
[19]2.2% methyl mercury dicyandiamide

was used during chamber inspection and watering to prevent the development of chlorophyll. Sprouts were harvested every 4 weeks, oven-dried and weighed. EG was expressed as mg/crown.

3.5 Regeneration Studies

3.5.1 Phenological Observations

3.5.1.1 Control Clones

Shrub growth and development were assessed at four to ten day intervals in 1981, and at seven day intervals in 1982. The onset and duration of leaf emergence, shoot elongation, flower bud development, flowering and fruit formation were monitored. General observations were made from each clone as a whole for all parameters except shoot elongation.

Shoot elongation was monitored by repeated measurement of tagged plants. Four "plants" in each of the control clones were randomly selected on a transect running north-south and spanning the southern clonal radius from apparent centre to the outside edge. Four branches on each plant were tagged with a loose fitting loop of brass snare wire. All current shoots on each branch were measured on each sampling date until shoot elongation ceased.

Rhizome extension was observed during bimonthly excavations made for the carbohydrate studies.

3.5.1.2 Mowed Clones

In addition to the phenological stages listed above, sucker emergence and elongation were monitored in regenerating clones. Duration of sucker emergence was determined by ocular estimation of sucker abundance rated on a four point scale (nil, few, frequent, abundant). When the abundant class was reached, sucker emergence was judged complete. This was verified by close inspection for newly emerging suckers.

Duration of sucker elongation was estimated by measuring two shoots near each of the ten sampling stations. On each sampling date, the length of the longest and shortest shoots was recorded. This technique was used since repeated measurement of suckers tagged at the beginning of the regrowth flush would not account for elongation of those suckers that emerged later on. This procedure was also followed in 1982.

3.5.1.3 Condition of Root Crown Buds

Root crown bud condition was rated on root crowns excavated from clones of the main study on October 27, 1981 and the strip mowed plots on November 7, 1981 and November 14, 1982. The ground was frozen to a depth of 10 to 20 cm by the autumn sampling dates. Sods with encased snowberry crowns were chopped from the frozen ground, thawed in the laboratory and washed free of sod and soil.

On the autumn sampling dates, observations were made with respect to:

a. presence or absence of elongating buds,

b. degree of elongation into shoots, and

c. site of bud origin, axillary buds on old stumps or basal buds on root crowns

Root crowns were excavated from the mowing study on May 4, 1982 when the ground was sufficiently frost free to permit field sampling. Previous and/or current season shoots were counted according to their position of origin on the root crown (axillary or basal). Any evidence of necrosis or desiccation on current sprouts was also noted.

3.5.2 Direct Estimation of Biomass, Annual Yield and Stand Structure

3.5.2.1 Background

Treatment effect on stand regeneration was evaluated in 1982 using the following parameters:

a. annual yield of snowberry composed of new wood, shoots, foliage and fruit,

b. annual yield of snowberry fruit alone,

c. annual yield of herbage,

d. plant density, and

e. stem density

Other stand parameters were quantified for interpretive purposes; including root mass, stem and root crown age.

In studies with herbaceous plants, responses are often based on current season yield of aerial biomass (Buwai and Trlica 1977, Sinton 1980). In woody plants, stands tend to be more variable, and current season yield includes not only shoots, leaves and fruit but new wood as well. The major problem is that new wood is tied up with old wood, from the previous season(s). Simple measurement of standing crop is appropriate to describe the resulting stand but not the annual yield.

The total dry matter yield of current season aerial biomass of western snowberry in 1982 (the first season following treatment) was estimated by subtracting standing crop of woody material, sampled the fall of 1981, from total standing crop of snowberry harvested in mid-August, 1982. Only four of the eight treatments had overwintering woody material. In August of 1981, 10 plots ($0.25m^2$) were randomly located in each clone and marked with wooden stakes. In clones that had overwintering stem material,

each random quadrat was paired with an additional plot, 1 to 2 m distant in a clone location of similar stem height and density. When the first plot harvest was made in September of 1981, 10 quadrats per clone were clipped by selecting one from each pair, alternately (1 random and then 1 paired), so as to balance out any biasing effect associated with the pairing process.

3.5.2.2 Plot Harvest – 1981

Ten quadrats, in each snowberry clone having regrowth (treatments A, B, C and E), were clipped between September 1 to 4, 1981. In control clones western snowberry, grasses and forbs were clipped and bagged separately. Samples were oven dried to a constant weight at 100°C. Snowberry samples were sorted to old stems and new shoots, with leaves and fruit combined. All shrub and herbage samples were weighed directly from the oven and tabulated as gm/m^2.

3.5.2.3 Plot Harvest – 1982

The final plot harvest occurred between August 16 to 23, 1982. In each control and treatment clone, the 10 remaining quadrats ($0.25m^2$) were sampled. Total plant numbers were determined prior to clipping. Old or new stems tended to occur in clusters on root crowns. Any stem or cluster of stems having 5 cm of basal separation from other stems was counted as a plant, based on the observation that stems originating from the same root crown rarely showed such spacing. As snowberry stems were clipped, the numbers of old live and dead stems and current live and dead sprouts were tallied. A 5 mm thick section was cut from all live stems of control clones for age estimation. Grasses and forbs were then clipped and all shrub and herbage components were bagged. After all live aerial biomass was harvested, snowberry root material was excavated from a vertical projection of the 0.25 m^2 quadrat. Five samples were taken per clone. All roots greater than 2 mm in diameter were separated from the soil to a depth of 60 cm. Root samples were spread out on fine mesh screen and washed free of soil and sod. A 5 mm section was cut from each distinguishable root crown for age estimation.

All samples were then oven dried and weighed as in 1981. Snowberry samples from control clones were sorted into old stems, new stems, leaves and fruit. Samples from treatment clones were sorted into two components namely fruit and all other fractions.

Root crown and stem sections were stained with a dilute solution of lactic–propionic orcein stain. Growth rings were then counted using a dissecting microscope. Drought and competition are major causes of interrupted cambial growth (Kramer and Kozlowski 1979). Since snowberry clones at the main study site were growing in full sunlight with mesic to hydric soil moisture conditions, false rings were assumed not to be a problem during age estimation.

The same overall procedure (1982 harvest) was carried out on the Frog Lake plots. Because of the small plot size, five frames (0.25 m^2) were randomly sampled in each of the three treatments. Estimation of annual yield did not include new wood and was based strictly on new shoots, foliage and fruit.

3.6 Statistical Analysis - Orthogonal Comparisons

By arranging single, double and triple cuts on all possible combinations of the three dates, *a priori* or orthogonal comparisons could be employed as the principal statistical procedure for testing treatment effect (Steel and Torrie 1980). Since clones were distinct individuals within each treatment, the experimental model was nested with experimental error partitioned between

a. TREATMENT

b. CLONES within TREATMENT and

c. error within CLONES

Planned comparisons were employed to test treatment effect on shrub sprouting reserves, shrub and herbage yield and shrub stand structure. Shrub yield is used below as

an example in listing the specific *a priori* questions posed.

1. Does season of cutting affect shrub yield?

2. Do shrub yield reductions differ with varied season(s) of single and double cutting?

3. Does frequency of cutting affect shrub yield?

4. Are added reductions in shrub yield derived from specific single versus double and double versus triple cutting sequences?

4. Results and Discussion

4.1 Environmental Conditions

4.1.1 Results

4.1.1.1 Air Temperature and Precipitation

In 1981, temperatures in late winter and early spring were higher than average (Table 3 and 4) with the last spring frost recorded on May 6 (Fig. 4). Monthly temperature means were near average for the balance of the season. The first autumn frost was recorded on September 3 (Fig. 4). Precipitation was below average in 1981, with growing season precipitation totaling 248 mm (Table 5). Monthly accumulations were 30 to 50% below average for all months except July, in which rainfall was 50% above average. Daily accumulations of rainfall are plotted in Fig. 4.

Climatic conditions during the second season of the study were substantially different from the first. The winter of 1981–82 was extremely cold (Table 4 and Fig. 8a). The lowest temperature of the winter was −46°C on January 2, 1982. Very cold conditions persisted well into the spring. The last frost was recorded on May 29 (Fig. 5). Monthly temperature means were near average, however, for June, July and August. Although overall growing season precipitation was slightly below average (315 mm), over 50% of the total fell in July (163 mm). Daily accumulations were so high in early July (Fig. 5) that soils were completely saturated, with surface ponding evident until the end of the second week of the month.

Table 3. Mean monthly temperatures (°C) at Beaverhill Lake in 1981, 1982 and 1974–80 average.

Month	1981[1]	1982[1]	1974-80[2]
January	-4.1	-24.3	-13.4
February	-6.6	-18.0	-11.0
March	.2	-10.0	-4.9
April	4.3	-1.2	4.6
May	12.4	7.8	10.4
June	12.3	14.0	14.1
July	15.7	16.6	16.3
August	17.4	13.0	14.0
September	11.4	–	10.5
October	2.3	–	5.7
November	-2.2	–	-3.1
December	-12.2	–	-11.5

[1]Data from the Alberta Energy and Natural Resources station, on-site.
[2]Data from the Tofield North Station, Atmospheric Environment Service, Environment Canada

Table 4. Mean monthly maximum and minimum temperatures (°C) at Beaverhill Lake in 1981, 1982 and the 1974–80 average.

Month	1981[1]		1982[1]		1974-80[2]	
	MAX.	MIN.	MAX.	MIN.	MAX.	MIN.
January	.7	-8.9	-19.0	-29.7	-8.7	-18.1
February	-1.4	-11.9	-12.0	-24.0	-6.3	-15.8
March	5.4	5.0	-3.8	-16.2	-1	-9.8
April	10.7	2.1	6.8	-9.2	10.2	-.9
May	19.6	5.3	14.7	.9	16.3	4.5
June	19.8	4.8	21.6	6.4	20.1	8.2
July	22.4	9.1	22.1	11.1	22.1	10.6
August	25.6	9.3	18.8	7.2	19.5	8.5
September	19.5	3.4	--	--	16.0	5.1
October	8.5	-3.9	--	--	10.8	.6
November	3.4	-7.8	--	--	1.4	-7.6
December	-6.7	-18.2	--	--	-8.4	-14.6

[1]Data from the Alberta Energy and Natural Resources station, on site.
[2]Data from the Tofield North Station, Atmospheric Environment Service

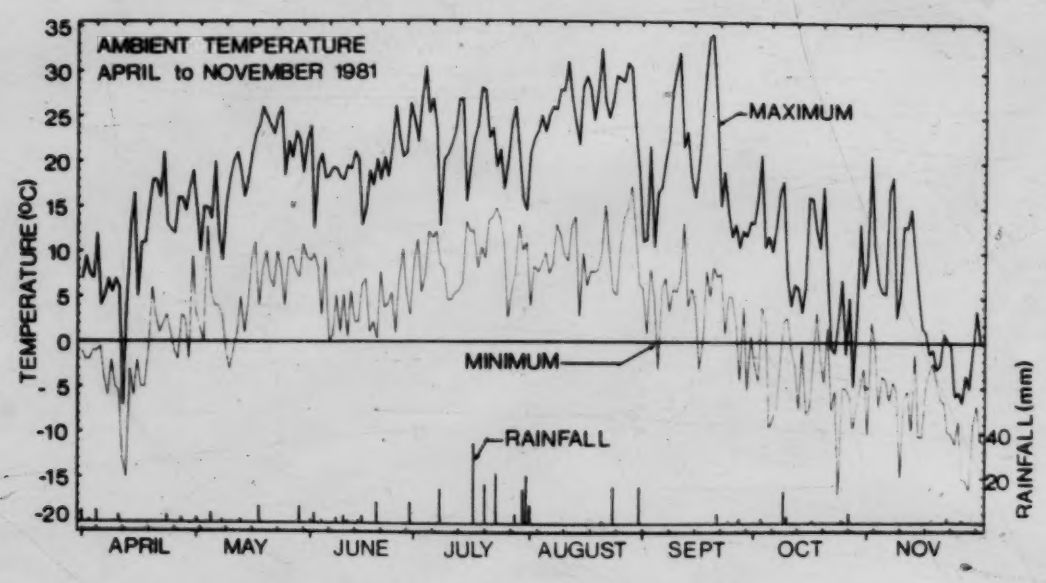

Fig. 4. Daily maximum and minimum air temperature and rainfall for April to November, 1981 at Beaverhill Lake.

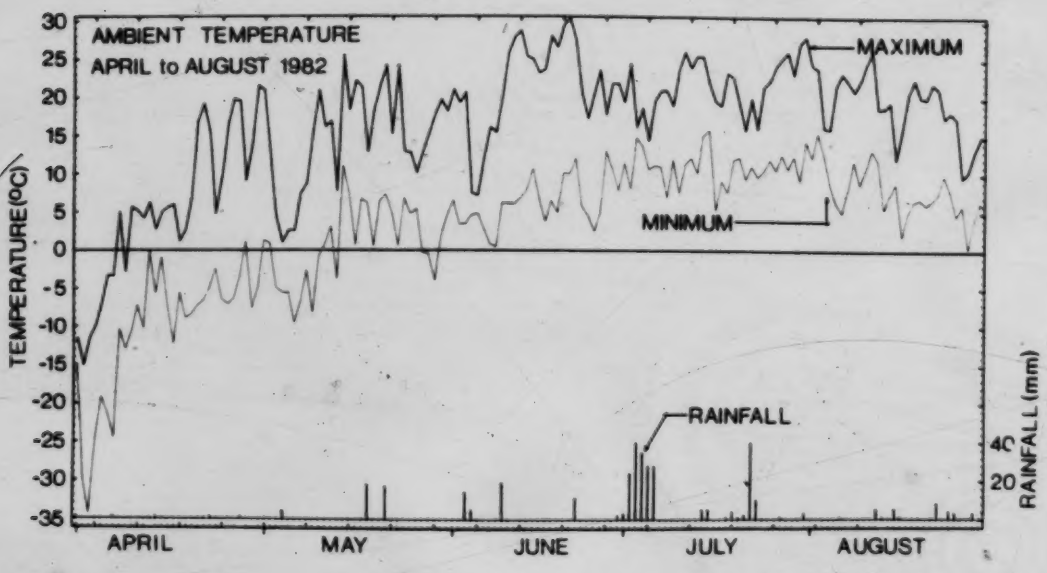

Fig. 5. Daily maximum and minimum air temperature and rainfall for April to August, 1982 at Beaverhill Lake.

Table 5. Monthly precipitation (mm) at Beaverhill Lake in 1981, 1982 and the 1974–80 average

Month	1981[1]	1982[1]	1974-80[2]
January	20	15	23
February	10	1	30
March	8	16	25
April	19	4	20
May	24	39	60
June	35	78	88
July	137	163	87
August	33	31	114
September	7	–	61
October	23	–	15
November	3	–	11
December	3	–	42
Total	322	–[4]	576
Growing[3] Season	229	311	349

[1]Data from the Alta. Energy and Natural Resources station on site.
[2]Data from the Tofield North Station, Atmospheric Environment Service
[3]Growing season was considered as April to August.
[4]Total for 1982 missing as station was shut down on August 28, 1982.

4.1.1.2 Effect of Mowing on Soil Temperature

Soil temperature values for both growing seasons of the study are plotted in Figs 6 and 7. Only values from the 5 cm depth are shown for 1981, because data from the 10 cm depth showed similar trends. Maximum soil temperature in the grassland was consistently higher than under shrub, in 1981. Differences on individual sampling dates ranged from 1 to 6°C, with the largest differences being evident in April and May. Soil temperatures under spring mowed shrub were intermediate between values recorded under grass or shrub cover. Higher temperatures in the spring-mowed shrub were not detected until three weeks after spring mowing and ranged from 1 to 4°C above those under shrub. The highest soil temperature values for the season were measured in the spring-summer cut, with values as high as 20°C and ranging from 1 to 5°C higher than under shrub.

In 1982, maximum temperature readings were monitored under shrub cover and late-summer mowed shrub only. The 1 to 3°C differences in soil temperature between cover types were comparable to those measured in 1981. Differences were not evident until late May after the final spring frost. The maximum soil temperature values measured in 1982 were 3 to 4°C lower than those recorded in 1981.

In the winter of 1981-82, minimum soil temperatures on the mowed site were consistently lower than under shrub cover (Fig. 8c). Soil temperature under both cover types declined steadily until January 3 and differed by 1 to 3°C. On this date, the lowest values for the winter were recorded as -13.5°C under shrub and -14.5°C under mowed shrub. After this date, soil temperature under the shrub rose sharply to -5°C with little fluctuation evident for the remainder of the winter. Under the mowed shrub, soil temperature fluctuated repeatedly, with temperatures ranging from 1 to 7°C colder than under the unmowed shrub.

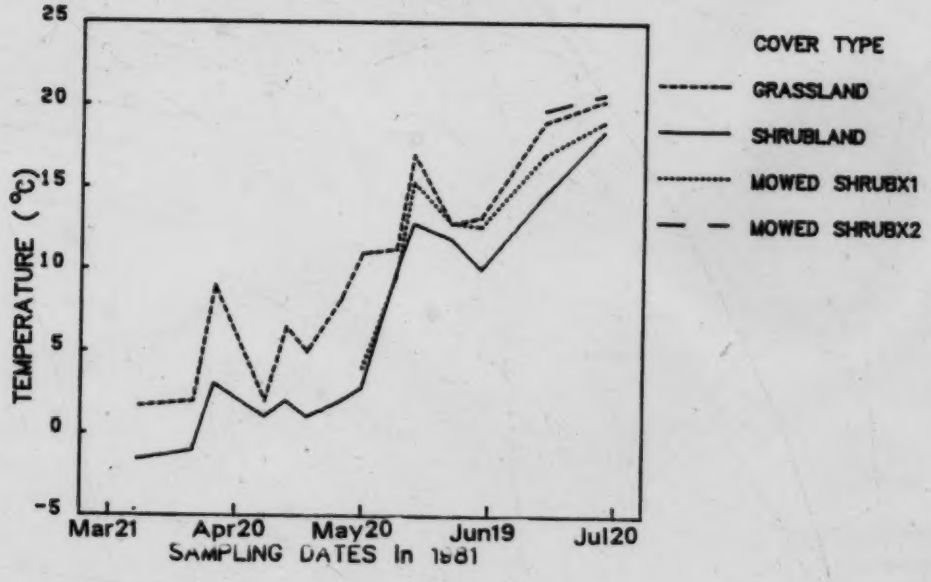

Fig. 6. Soil temperatures at 5 cm, under four cover types, in 1981.

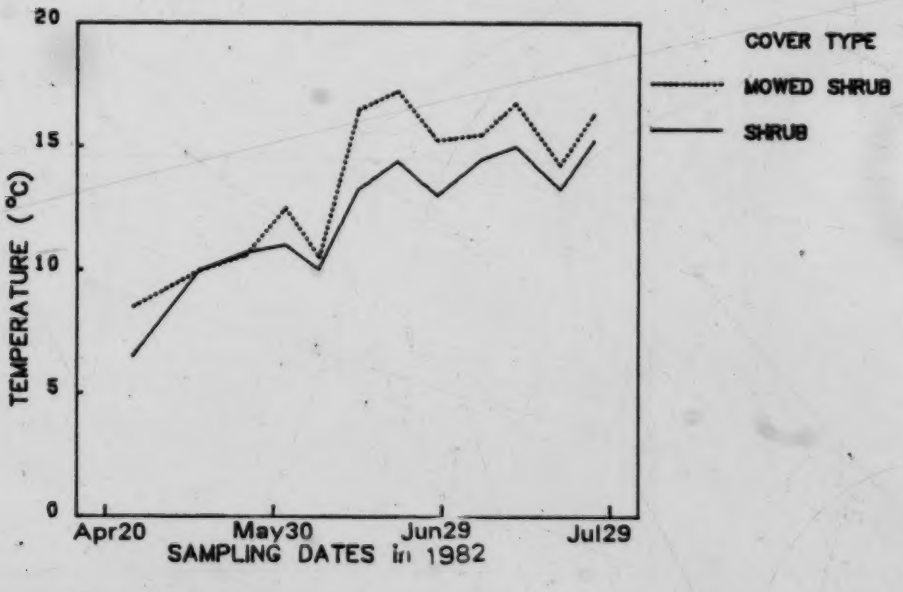

Fig. 7. Soil temperature at 5 cm, under two cover types, in 1982.

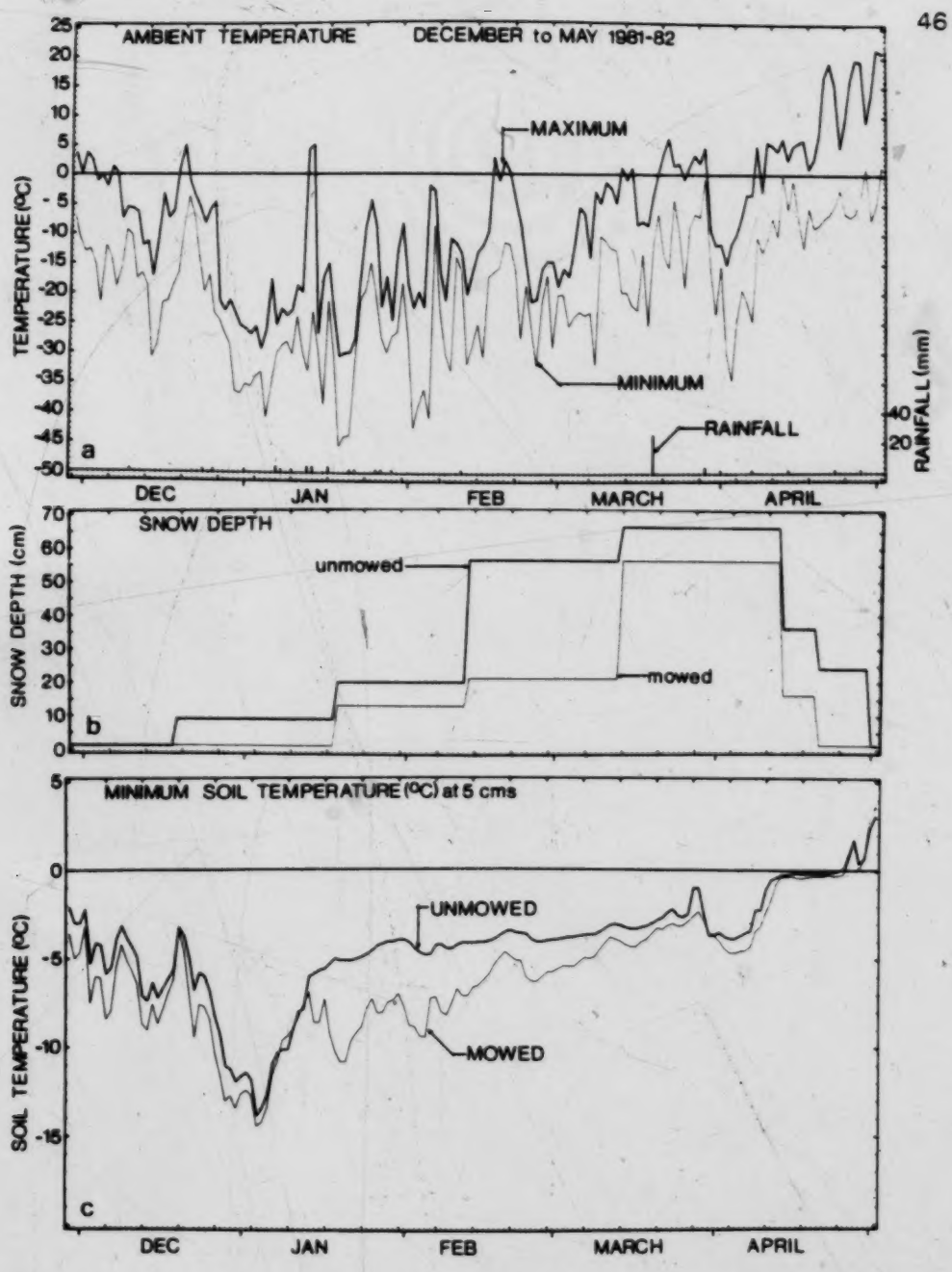

Fig. 8. Daily maximum and minimum air temperature and precipitation (rainfall equivalent) with snow depth and soil temperature (at 5 cm) by mowing treatment during the 1981-82 winter at Beaverhill Lake.

A treatment effect on snow accumulation has obvious implications for winter soil temperature (Fig. 8b). Very little precipitation fell in December 1981 (Fig. 8a). Most snow that fell tended to drift into shrub stands. Although substantial amounts of snow fell in January and February, snow accumulation on the mowed shrub sites was delayed until March. Retention of snow on mowed sites after mid-March was likely due to crusting initiated by brief thaws. Not only was snow accumulation delayed on the mowed shrub, but melt-out came 1 to 2 weeks earlier than in the unmowed shrub.

4.1.1.3 Effect of Mowing on Soil Moisture

When soil moisture data gathered in 1981 were analysed, DATE and TREATMENT effects were significant (Appendix 2-B). However, when the overall means for treatments were tested, there were no significant differences (Table 6). The overall mean for grassland soil moisture was significantly less than 4 of the 8 treatment means.

In the spring of 1981, on the first sampling date, soil moisture averaged 47% by weight, overall (Fig. 9). Soil moisture levels under control and mowed snowberry remained above 25% until well after the major period of growth. Soil moisture was lowest under grassland cover, dropping to below 20% one month sooner than under control or mowed shrub stands.

In 1982, soil moisture was monitored in control and late-summer cut shrub. Problems arose in sampling the deepest horizon in two of the sample tubes (i.e. crimped pipe) and, consequently, horizon three was omitted from the data matrix. There were significant effects due to TREATMENT, HORIZON and DATE (Appendix 2-C). The overall reduction in soil moisture was significant in the upper horizon (4%) but not in the lower (0.7%, Table 7).

The soil moisture means for TREATMENTxDATE are presented in Fig. 10. Although early season precipitation was below average, soil moisture levels during this period were adequate to support growth. Because of heavy rainfall in July,

Table 6. Effect of treatment on mean soil moisture (% by wt, 0 to 15 cm depth), sampled on five dates in 1981.

Treatment		% Soil Moisture[1]
A	Control	29.1ab
B	Spring	27.2ab
C	Summer	30.1a
D	L. Summer	27.4ab
E	Spr.–Sum.	28.0ab
F	Sum.–L.Sum.	31.3a
G	Spr.–L.Sum.	30.1a
H	Spr.–Sum.–L.Sum.	29.5a
I	Grassland	24.8b
	S.E.[2]	(1.1)

[1]Means followed by the same letter are not significantly different (Student–Newman–Keuls test, $p<0.05$).
[2]Refers to the standard error of the means.

mean soil moisture values ranged above 25%.

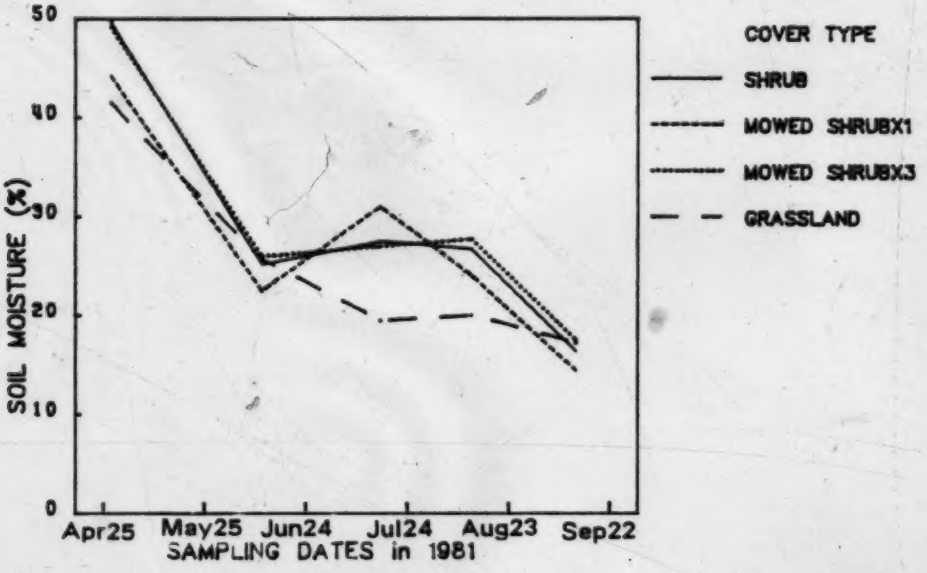

Fig. 9. Soil moisture in the surface 15 cm, under four cover types, in 1981.

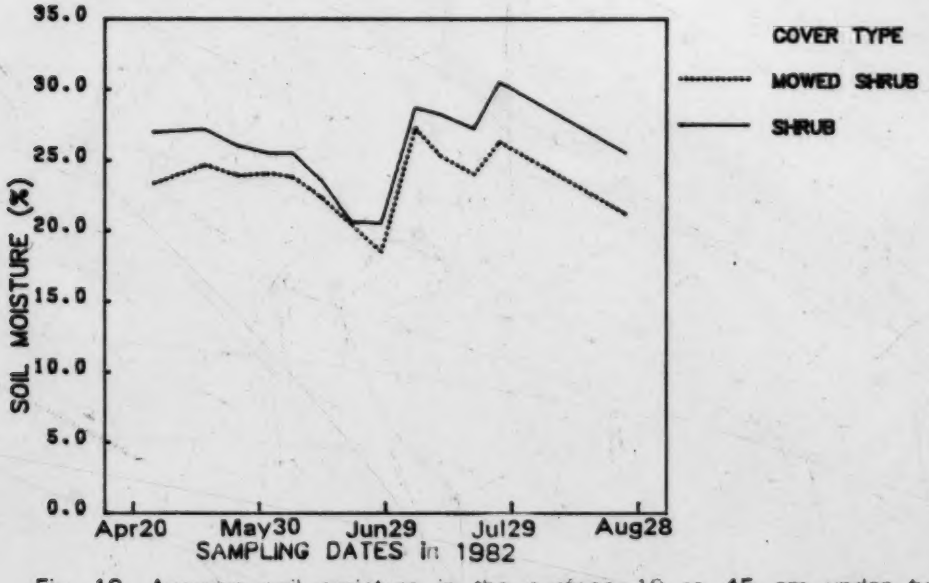

Fig. 10. Average soil moisture in the surface 10 to 45 cm under two cover types, in 1982.

Table 7. Effect of treatment on soil moisture (% by wt.), at two depths and overall means[1] of readings made on 12 dates in 1982.

Treatment	Horizon 1[2]	Horizon 2[3]	Mean[4]
Shrub	26.0a	25.6a	25.8a
Mowed shrub[5]	22.0b	24.9a	23.5b
S.E.	0.8	0.8	0.2

[1]Means within columns followed by the same letter are not significantly different (SNK test, $p<0.05$).
[2]Readings made at the 10 to 25 cm depth.
[3]Readings made at the 30 to 45 cm depth.
[4]Mean soil moisture with both horizons combined.
[5]Monitored in clones that were mowed in 1981.

4.1.2 Discussion

First year climatic conditions can be summarized as normal for temperature and below average for spring precipitation. Soil moisture appeared to be in adequate supply throughout the growing season. During the second year, spring temperatures were below average, the season was delayed by 3 weeks and midseason precipitation was extremely high. First year growing conditions were average, while those of the second year would be expected to favour vegetative growth since moist and cool conditions tend to delay flowering (Kramer and Kozlowski 1979).

Soil temperature may influence woody sprout emergence (Schier 1976). Results reported here show that soil temperature increased as the season progressed, regardless of cover type, and that temperatures were higher under mowed snowberry than under shrub. Therefore, the timing of sprout emergence in relation to these season and treatment related effects may influence stem density in regenerating stands.

In winter hardiness studies, the severity of winter conditions is related to the amplitude, fluctuation and duration of low temperatures (Levitt 1980). If a particular treatment would have reduced winter hardiness in western snowberry, the winter of 1981-82 should have been an excellent one to cause winter injury. Snowberry mowed in late-summer was subjected to greater extremes, greater fluctuations and longer duration of cold temperatures than was the unmowed shrub. In effect, mowing altered the winter environment and made conditions more severe.

Mowing during the first year had no obvious effect on soil moisture. It also seems likely that soil moisture was not a factor limiting growth in either year of the study. In 1982, the overall reduction in soil moisture between mowed and control cover types likely related to lesser snow accumulation in the former. The lower soil moisture levels in the grassland during the summer of 1981 may also have reflected the influence of shrub cover on snow accumulation.

4.2 Phenology

4.2.1 Results

Phenological observations were recorded on a clonal basis (Fig. 11). There was a variation between clones of one to seven days in the onset and duration of phenological events. The summaries presented in Fig.s 12, 13 and 14 were derived by averaging the observations from the four clones in each treatment, and employed the graphical approach of Larcher (1980).

4.2.1.1 Phenology of Control Clones

In control clones, the onset and duration of vegetative events differed between 1981 and 1982, while the timing of reproductive events was nearly identical. The date of spring leaf bud emergence differed by two weeks between years, commencing on April 14 in 1981 and May 2 in 1982. In 1981, shoot elongation began during the first week of May, and persisted for 6 weeks. In contrast, shoot elongation began one week later and continued for 8.5 weeks in 1982. Although flower bud development commenced earlier in 1981, the onset of flowering and fruit swelling did not differ between years. Anthesis commenced on June 26 in both years, with fruit swelling apparent three weeks later. The first sign of newly produced rhizomes (fleshy and white) was in mid-June of 1981 and rhizome extension appeared complete by August. Leaf senescence and abscission were gradual and commenced in early September. Many clones retained their leaves, though curled and discolored, well into early winter.

Kentucky bluegrass, the dominant grass species within the control clones, exhibited an etiolated appearance. Leaf blades were long (30 to 50 cm) and pale green in color. Few plants produced seed heads.

Fig. 11. Major phenological stages of western snowberry: (A) bud release, leaf emergence and leader elongation (B) flowering (C) fruit formation (D) mature plant in fruit (E) juvenile plant sprouting from a rhizome.

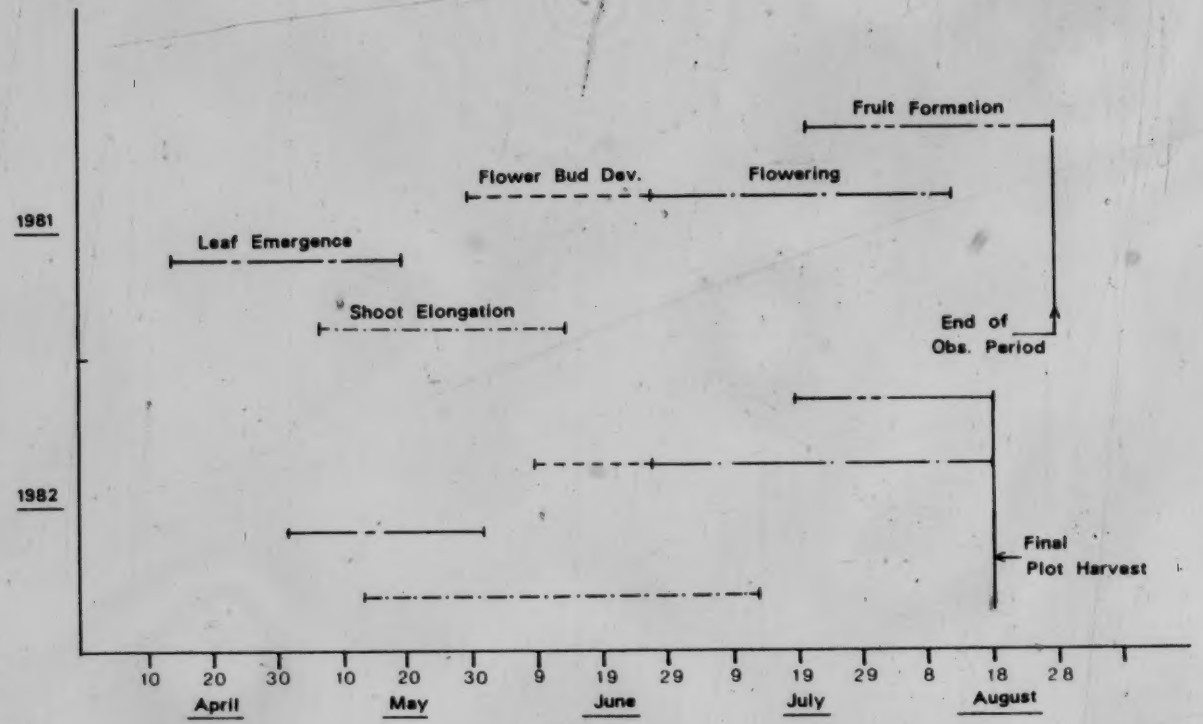

Fig. 12. Phenology of western snowberry during 1981 and 1982 in control clones.

4.2.1.2 Phenology of Regenerating Clones

Phenology of the control and regenerating snowberry clones is summarized by treatment, for the year of mowing (Fig. 13), and for one season after treatment (Fig. 14). In general, mowing treatments altered the onset and duration of vegetative and reproductive development. In 1981, vigorous resprouting and growth were observed in single and double cut treatments mowed in spring or early summer. New sprouts emerged over a period of 4 to 5 weeks after cutting on the first date and in those clones cut again on the second date. The sprout emergence interval was shorter (3 weeks) in clones cut for the first time in midseason. Resprouting after the second cut, regardless of treatment, was less vigorous than the growth flush which followed the first cut. There were no above ground signs of resprouting after cutting on the third date.

The single spring cut (B) was the only mowing treatment in which snowberry not only resprouted, but flowered and produced fruit. Minor flower bud swelling was detected in the spring–summer double cut (E). Although fruit swelling was observed in the single spring mow, only about 20% of these fruit ripened. In October the remaining berry primordia appeared shrivelled and frost damaged.

Regardless of the season or frequency of mowing, sprouts from clones defoliated prior to the late summer cut rebranched and produced secondary shoots from July 22 to 28. In control clones, a single flush of shoots was observed. By the fall of 1981, treatments B, C and E had regained varying amounts of woody standing crop.

No sign of rhizome elongation was observed in any of the spring or summer cut treatments.

During the first post cutting interval in each mowing treatment, there was a prolonged delay in tillering of Kentucky bluegrass, relative to western snowberry. In spring and summer cuts, snowberry sprouts were emerging before the first new bluegrass tillers were evident.

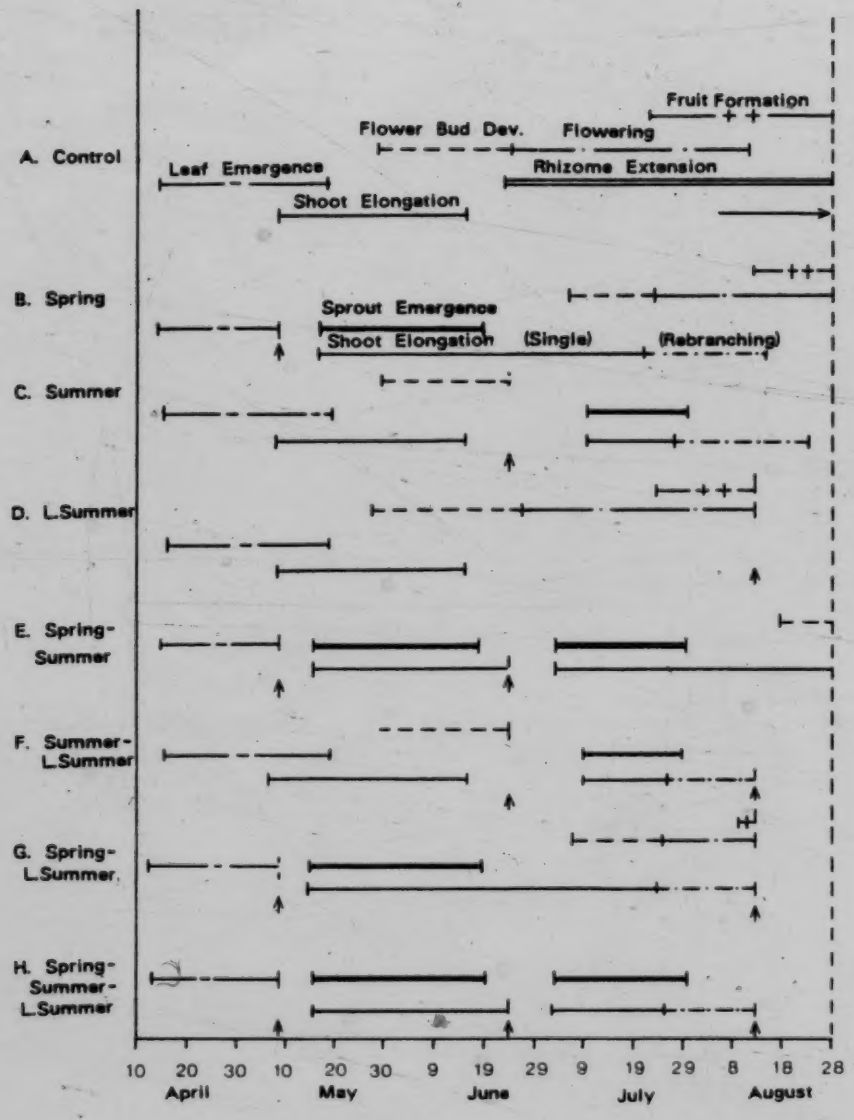

Fig. 13. Average effects of season and frequency of mowing on the phenology of Western snowberry in 1981 (↑ depicts mowing dates).

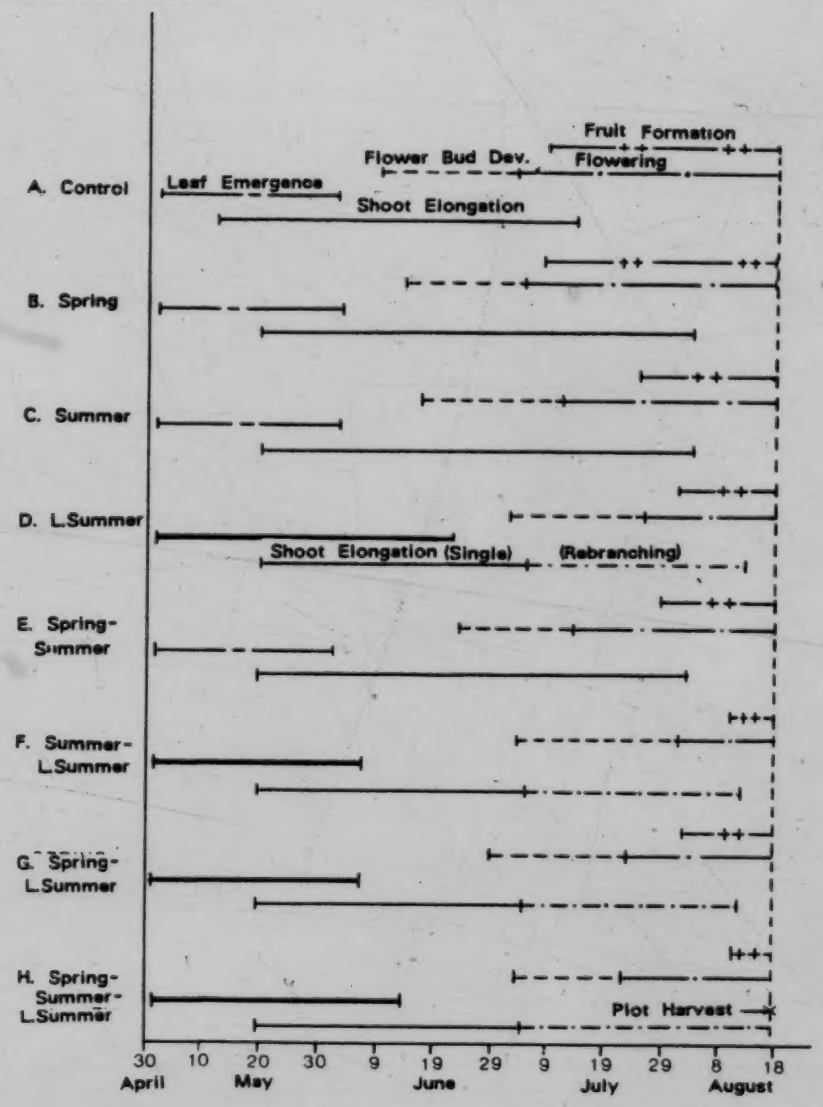

Fig. 14. Average effects of season and frequency of mowing on the phenology of western snowberry in 1982.

On May 2, 1982, growth resumed in all treatments. The duration of sprout emergence in the summer-late summer (F) and spring-late summer (G) cuts was five weeks, this being similar to the emergence interval in the spring of 1981. Sprout initiation was prolonged by an additional one week in the triple cut (H) and by two weeks in the single late summer cut (D). As compared to control clones, shoot elongation was delayed by three weeks in those mowing treatments with overwintering stem material (B, C, E) and five weeks for those regenerated from ground level (D, F, G, H). Snowberry clones which resumed growth from overwintering stems, produced a single flush of new shoots. All clones which sprouted from ground level (D, F, G, H), rebranched during the first week of July.

Flower bud emergence, flowering and berry formation were notably delayed in all mowing treatments. Flowering was particularly delayed in those treatments that commenced growth from ground level, in the spring of 1982.

4.2.1.3 Condition of Root Crown Buds

There were treatment related differences in vegetative bud release. It was found during excavation of root crowns on October 27, 1981 that shoots arising from axillary buds had emerged above the soil surface in all late-cut treatments (D,F,G,H). These expanded buds emerged immediately below the cut surface of the stump, appeared injured by frost and were 5 to 10 mm long. The most striking treatment effect, though, was observed on root crowns from the single late-summer cut (D). A conspicuous flush of late season sprouts was apparent (Fig. 15a). Not only did buds emerge at the collar of the old stump but also from basal sites as far down as the region of stem-root crown interface. These late released sprouts were swollen and white, ranging in length from 1 to 5 cm. At the time of excavation only those sprouts that had broken the soil surface, were green tipped and in the initial stages of leaf emergence, appeared necrotic (Fig. 16 a, b and c). Approximately 30% of the released buds exhibited desiccation or frost injury symptoms, primarily those sprouts arising along the stump in the surface 0 to 5 cm.

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Fig. 15. Snowberry root crown samples showing bud release (a, cut Aug. 6 + 13) and bud swelling (b, cut Aug. 20).

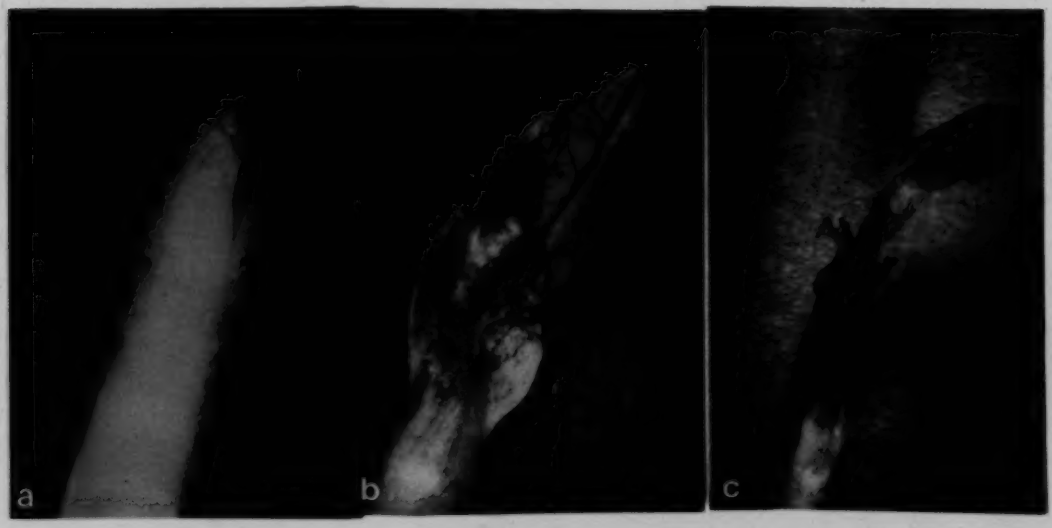

Fig. 16. Snowberry buds released with late cutting. Frost injury increased with the degree of bud burst.

No visible signs of bud release were observed in any of the other treatments (A, B, C, and E).

The condition of root crown buds, in the strip mowing plots that were cut at weekly intervals in August, was similar to that observed in the single late cut treatment. However, bud release diminished with progressively later cutting dates (Table 8). Bud condition was identical in the August 6 and 13 cuts to that described already for the single late season cut. Stump sprouts were not apparent on root crowns from strips mowed on the subsequent cutting dates. In the August 20 cut, buds on root crowns were swollen and spheroidal but not elongated (Fig. 15b). Vegetative buds remained covered by scales on samples excavated from the August 27 and September 3 cuts.

In the spring of 1982, the bud conditon of root crowns was similar to that observed the previous autumn. An attempt was made to count the frost injured (Fig. 16 b and c) and surviving (Fig. 16 a) sprouts.This procedure was unsuccessful. Injured buds were, in fact, observed, but owing to their fragile nature, could not be satisfactorily counted. Desiccated buds tended to snap off during the separation of sod from root crowns.

Since bud mortality could not be satisfactorily assessed, an alternate approach was taken to quantify the possible influence of the treatment effect on vegetative buds. In the single late-summer cut, new shoots appeared to originate predominantly from basal positions. When shoots, produced currently or in the previous season, were counted according to their site of origin, the single late cut had the highest proportion arising from basal positions (Table 9, Appendix 2-D). A predominance of basal sprouts was interpreted to reflect the view that frost injury of axillary buds necessitated the production of new sprouts from buds on the root crown and not the stump.

With spring or summer cutting new sprouts arose from axillary buds on the upper stump. In multiple cut treatments, sprouts arising subsequent to the first cut,

Table 8. Summary of fall bud condition on root crowns excavated from strip mowed plots, on October 27, 1981.

Mowing Date	Bud Condition	Bud Length(cm)	% Injury
August 6	bud release evident -on stump collar -stump collar to stump base	 0.5-1 1-5	 100% 30%
August 13	bud release evident -on stump collar -stump collar to stump base	 0.5-1 1-5	 100% 30%
August 20	bud swelling only -stump collar to stump base -buds white and spherical	0.1-0.2	nil
August 27	no release or swelling -buds remain scale covered	<0.1	nil
September 3	no release or swelling -buds remain scale covered	<0.1	nil

Table 9. Percentage[1] of post treatment shoots by site of origin, on May 2, 1982

	Treatment	Stump[2]	Root Crown[3]
B	Spring	94	6c
C	Summer	64	37b
D	L.Summer	41	59a
E	Spr.-Sum.	91	9bc
F	Sum.-L.Sum.	78	22bc
G	Spr.-L.Sum.	85	15bc
H	Spr.-Sum.-L.Sum.	88	12bc
	S.E.	7.1	7.1

[1]Means followed by the same letter are not significantly different (Student-Newman-Keuls test $p<0.05$).

[2]shoots arising from axillary buds.
[3]shoots arising from basal buds.

tended to originate from currently initiated buds, produced at or near the base of the first sprouts. But, with the single late summer cut, shoots arose from distinctly more basal positions. Currently initiated buds formed at the base of shoots released with spring or summer initial cuts. These currently initiated buds provided the major bud supply for subsequent sprouts when second or third cuts were applied. In the single late-summer cut, frost injured a portion of the buds that had been released. Currently initiated buds did not form at the base of these injured sprouts. Therefore new sprouts originated from dormant buds of distinctly more basal sites of origin.

Sequential cutting in the strip mowing plots was repeated in 1982. Observations in the spring of 1982 indicated that sprout injury was related to the degree of emergence. Initially it seemed logical to move cutting dates forward into late July to enhance sprout emergence and hence vulnerability. However, since the 1982 growing season differed considerably from 1981, the same dates were employed in the event that seasonal variation produced a different effect. Vegetative buds on samples excavated from the strip mowed plots showed the same date-related gradient in bud release as portrayed for 1981 in Table 8.

4.2.2 Discussion

Most temperate shrubs have a minimum chilling requirement necessary to break winter bud dormancy. These requirements may be met after weeks or months of exposure to cold temperatures, after which quiescence is said to be environmentally imposed (Kozlowski 1971a). Bud break and shoot outgrowth may then proceed with rising soil and air temperatures (Lavender 1980). In both years, bud break commenced within 4 to 5 days of frost leaving the soil surface. Marked shoot elongation was not observed, however, until mean daily temperature reached 5 to 10°C.

Shoot outgrowth is normally limited by internal factors (Lavender 1980). Anatomical stem units may be completely preformed in overwintering buds (Lanner 1971). Mature snowberry plants appear to have a "fixed" rather than "free" shoot growth pattern because only a single flush of new shoots was observed in control clones. The extended

duration of shoot elongation in 1982 seemed to relate to cool spring conditions and extremely high mid-season precipitation, thus favouring vegetative growth. Higher snowberry yields in control clones during 1982 correspond to these differences in climate and phenology.

Although flower bud initiation differed slightly between years, flowering in both years commenced less than one week after the longest day (June 22). Pelton (1953) reported a strong photoperiod related flowering response in snowberry plants exposed to long days. A reduction in daylength below the maximum for the latitude in question halted further flowering and normal vegetative growth.

Possible reasons for the late-summer elongation of rhizomes observed here are unclear with little information being available in the literature. Since rhizomes are true subterranean stems, it is unlikely that they are induced to grow by the same stimuli as roots. The elongation of rhizomes late in the season may relate to the seasonal decline in auxin (and hence release from apical dominance) and/or an increase in NSC to fuel growth as sink demands decline in other regions. A possible explanation may be tied to the seasonal trend of increasing soil temperature. The highest growing season temperatures in the surface 5 cm corresponded with the major period of rhizome extension. The destruction of auxin may be enhanced with a higher soil temperature regime (Schier 1976) permitting the release of rhizome apices from apical dominance.

Mowing of western snowberry removed the apical dominance exerted by stems on the vegetative buds. Two substantial waves of sprouts followed single and double cuts made in spring and early summer. Since soil moisture levels remained above 20%, the failure of late mowed clones to regenerate was not the result of drought-enforced dormancy. Furthermore, the final cut was timed to be well into the period associated with dormancy induction (McKenzie and McLean 1980a). The lack of regeneration after this date may be in part linked to growth inhibitors produced by the plant under the influence of short days. It is, however, more likely that the relative balance of growth promoter(s) to inhibitor(s) is responsible, especially in light of the condition of fall buds.

Late released sprouts were produced in the single late cut alone. Schier (1979) reported a similar end-of-season bud condition in aspen plants where stem decapitation occurred for the first time during the induction of dormancy. Bud release was not evident in other treatments where additional cuts were applied prior to the mid-August mowing. In this study the multiple cut treatments had more juvenile foliage at the time of the final mowing, and therefore it seems unlikely that inhibitor production is solely responsible for the lack of bud release. In *Acer pseudoplatanus* L., photoperiodic perception is strongest in mature leaves (Wareing 1956, Phillips *et al*. 1980). If inhibitor production was solely responsible, the greatest inhibition in sprout release would likely have occurred in the single late cut, this treatment having the oldest leaves at the time of mowing. Differences in cytokinin production may account for the contrast. Defoliation reduces root growth (Kramer and Kozlowski 1979, Eliasson 1971b) and therefore cytokinin production is apt to be reduced also. A lower stimulus for vegetative bud release would appear to be the consequence. The marked bud release in the single late cut would similarly be expected since normal root growth would have occurred up to the time of defoliation and endogenous cytokinin levels would be expected to be higher than in those treatments defoliated on earlier dates.

The juvenile stage of regenerating snowberry displayed a consistent "free" growth pattern, with midseason rebranching of primary sprouts observed in all snowberry clones. Kramer and Kozlowski (1979) noted that if the root to shoot ratio is changed by defoliation, compensatory growth will result to restore the characteristic balance. The difference in rebranching dates between years may have been influenced by the effect of between-year variation in precipitation on endogenous cytokinin levels. Browning (1973) reported an increase in cytokinin levels in *Coffea arabica* L. in response to irrigation or rainfall. In both years of the study, the week prior to rebranching was characterized by high rainfall levels (Figs. 4 and 5).

Floral induction in temperate shrubs such as snowberry is related to high rates of photosynthesis, long days and adequate levels of nutrition (Kozlowski, 1971b). In control clones, these essential requirements were obviously met since flowering commenced on

the same date in both years with fruit forming, shortly thereafter. In 1981, the single spring cut (B) was the only treatment in which snowberry was able to regenerate sufficiently to produce fruit. Even so, heavy demands for carbohydrate for vegetative regeneration, may account for the fact that, relative to the control, only about 20% of the flower buds that reached anthesis, produced mature fruit. Leaf area was clearly a critical factor, since fruit production in 1982 appeared to be proportional to the amount of stem regeneration left to overwinter. Logically, those plants which had a greater standing crop of stem material, in the spring, would also establish a larger leaf area in spring and be able to produce more NSC.

It is unlikely though that the abortion of the fruit crop was simply the result of sink competition for carbohydrate. As mentioned in previous paragraphs, hormone levels may have been altered by mowing. Without normal hormonal stimuli fruit filling would not occur (Kramer and Kozlowski 1979).

The implications of treatment effect on phenology will be discussed further in subsequent sections.

4.3 Seasonal Variation in Nonstructural Carbohydrate and, Sprouting Reserves

4.3.1 Results

4.3.1.1 Statistical Analysis

The experimental model and analysis of variance for each of the seasonal NSC and sprouting reserve studies are presented in Appendix 2-F, G, H, and I. Where the seasonal trend in NSC for control and spring mowed clones was portrayed, statistically significant differences between dates were interpreted visually from the plotted confidence intervals.[20] Differences between dates are significant if confidence intervals do not overlap.

Where the effect of season and frequency of defoliation on fall levels of NSC and EG was evaluated, data were analysed by the method of least squares[21]. The *a priori* questions (outlined in Chapter 3) were tested with an orthogonal contrast procedure (Steel and Torrie 1980). An APL-Orthogonal Comparsion[22] package was used to derive test values. The error mean square of "CLONES within TREATMENT" formed the valid error term for testing the sums of squares derived for each comparison.

4.3.1.2 Effect of Season on Nonstructural Carbohydrate in Control Clones

George and McKell (1978a) failed to detect a significant reduction in root crown NSC levels in *Symphoricarpos oreophilus* Gray during the first season of defoliation treatment. They found that assessment of NSC in other plant fractions was required to detect seasonal changes and treatment effects. Therefore, this study included sampling of large root and stem fractions in addition to root crowns. Effects due to PLANT COMPONENT, DATE and COMPONENTxDATE interaction were significant (Appendix 2-F). The seasonal variation in root crown NSC is portrayed in Fig. 17.

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[20]The 95% confidence intervals are calculated as 2xS.E.xto (to=2.365 for $p<0.05$, 7 d.f.).
[21]A. Mellenbacher DESMAT and LSQANOVA, Dept. of Animal Science, Univ. of Alta.
[22]W.L. Smillie, University of Alberta, Dept. of Computing Science.

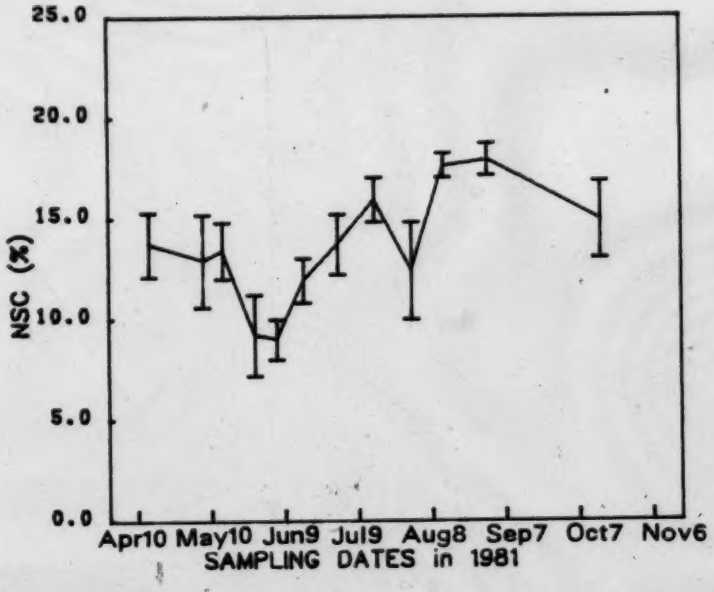

Fig. 17. Seasonal variation in root crown NSC (%) in control clones of western snowberry during 1981 with a 95% confidence interval.

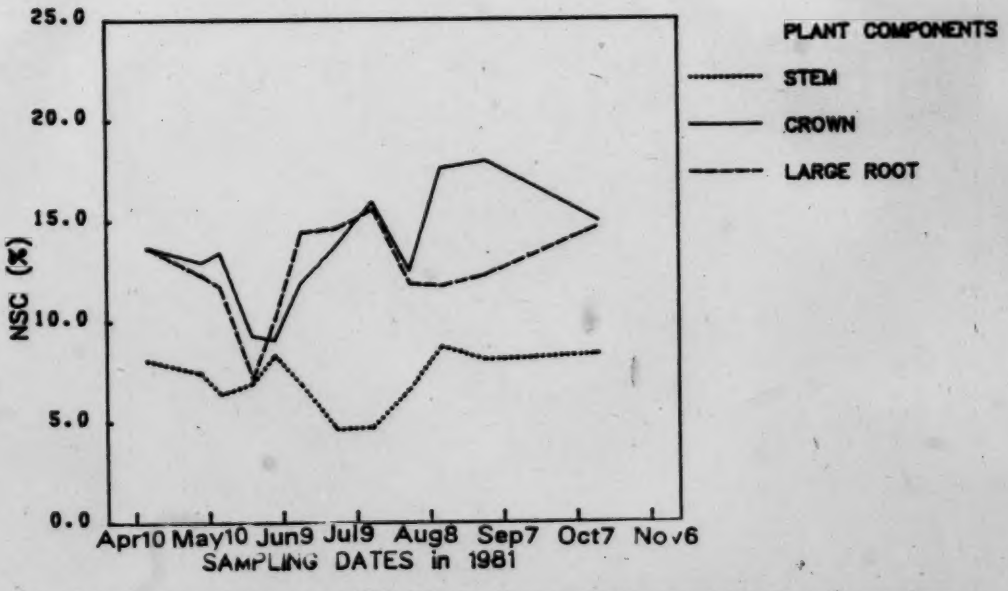

Fig. 18. Seasonal variation in NSC (%) in three plant components of western snowberry control clones in 1981.

In control clones, the period of maximum drawdown in root crown NSC corresponded with the stage of 2/3 shoot elongation. Draw-down in NSC levels commenced about May 15. The seasonal low, which was significantly less than the initial spring level, was reached by May 28. The low persisted for 10 days, and was followed by a rapid recharge that peaked around July 16, 2-3 weeks after flowering had commenced. Duration of the period of recharge in root crowns was approximately 40 days. A further dip in NSC levels was observed during the onset of fruit swelling. After this, reserve levels were quickly replenished towards an autumn high, which were significantly higher than in spring. A further gradual decline was evident from late August to mid-October.

Seasonal variation of NSC in stem, large root and root crown fractions are plotted in Fig. 18. The correlation between seasonal NSC values in root crowns versus large roots was significantly positive ($r=0.56$, $p<0.05$) while that between root crowns and stems was significantly negative ($r=-0.68$, $p\leq0.05$). Changes in stem NSC levels tended to be opposite to those in other fractions. As growth and development progressed, NSC depletion in the large root and root crown fractions was countered by NSC recharge in the stem fraction and vice-versa. Stem NSC remained virtually unchanged after the onset of fruit filling. Root crown and large root fractions differed significantly in their respective NSC patterns after the major period of fruit development (late August to mid-October). The sharp increase in root crown NSC following fruit swelling was contrasted by slow, gradual recovery in the large root fraction.

4.3.1.3 Effect of Spring Mowing on Seasonal NSC Levels

When the data comparing the effect of spring mowing on the seasonal NSC cycle were analysed, all terms in the experimental model were significant (Appendix 2-F). A single spring mowing during the time of leaf expansion produced a significant overall treatment effect on seasonal reserve levels. The significance of DATE and DATExTREATMENT interaction is of key importance. The DATE effect implies that NSC levels varied significantly over the season regardless of treatment.

The DATExTREATMENT interaction indicates that seasonal patterns in the respective treatments were distinctly different. The seasonal NSC means for the 12 sampling dates are plotted in Fig. 19. Subsequent to spring mowing, rapid draw down in NSC was accompanied by a vigorous flush of sucker regrowth. The mean seasonal low was reached by May 28 and lasted until July 16, a total of just over 6 weeks. At the time of recharge, which took place within a three week period, snowberry sprouts had reached an average height of 40 cm with 11 leaf pairs. By autumn, NSC levels in spring mowed clones had been recharged to spring levels. The differences in the seasonal NSC patterns of control and spring mowed clones are compared in Fig. 20.

4.3.1.4 Effect of Treatment on Fall Sprouting Reserves

The treatment means for fall NSC reserves are portrayed in Fig. 21. The results of orthogonal contrast testing are presented in Table 10. Summer and late-summer single cuts reduced autumn NSC to levels significantly lower than the control (comparison(C) 1, 2 and 3). Differences between single cuts were not significant (C 4, 5 and 6). In the single cuts a season effect was apparent in the trend towards lower autumn NSC levels with progressively later cutting dates (Fig. 21).

The season effect derived in single cuts was also obvious in the comparison of double cuts (C 7, 8 and 9). Those with a late-summer second cut had significantly lower NSC levels than the spring-summer cut. The average reduction from single cutting compared to that of double cutting was not significant (C 11) while that from double versus triple cutting was (C 12).

Significant added effects were derived from spring or summer initial cuts with a late-summer follow up (C 13, 14, 15 and 16). Triple cutting produced significant additional NSC reductions regardless of the season of the double cuts (C 17, 18 and 19). In short, NSC were reduced with progressively later and increased frequency of cutting.

In the etiolation study, the measure of regrowth potential was based on the outgrowth of sprouts grown in the dark from excised snowberry root crowns. As with NSC reserves, EG reserves also displayed a spectrum of depletion (Fig. 22).

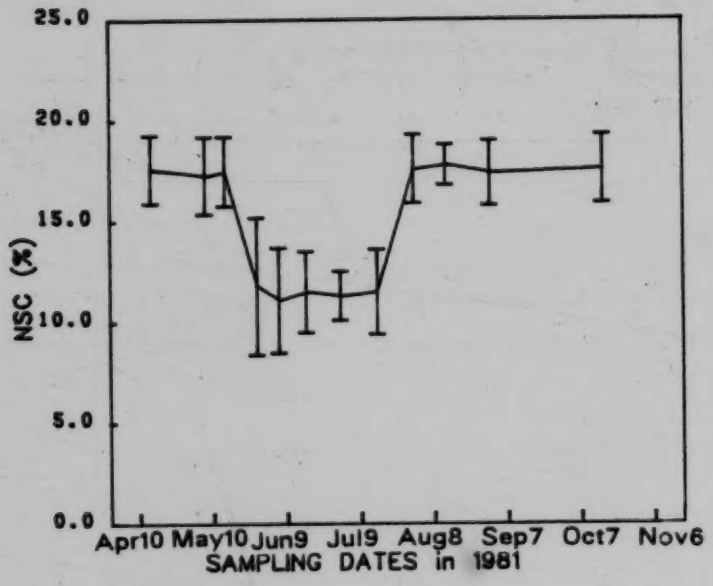

Fig. 19. Seasonal variation in root crown NSC (%) in spring mowed clones during 1981, with a 95% confidence interval.

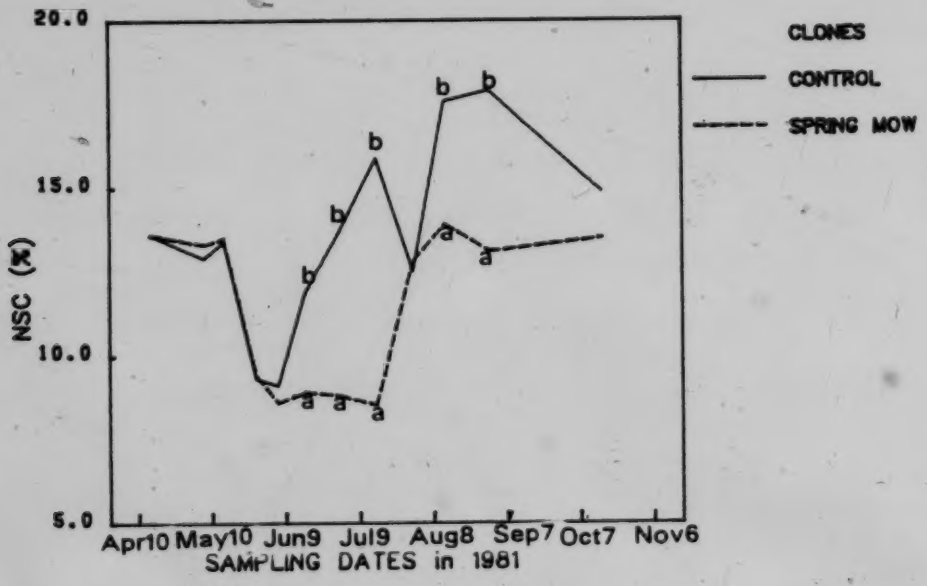

Fig. 20. Comparison of seasonal variation in root crown NSC (%) between control and spring mowed clones. Differences for the same dates between treatments are significant where indicated by different letters.

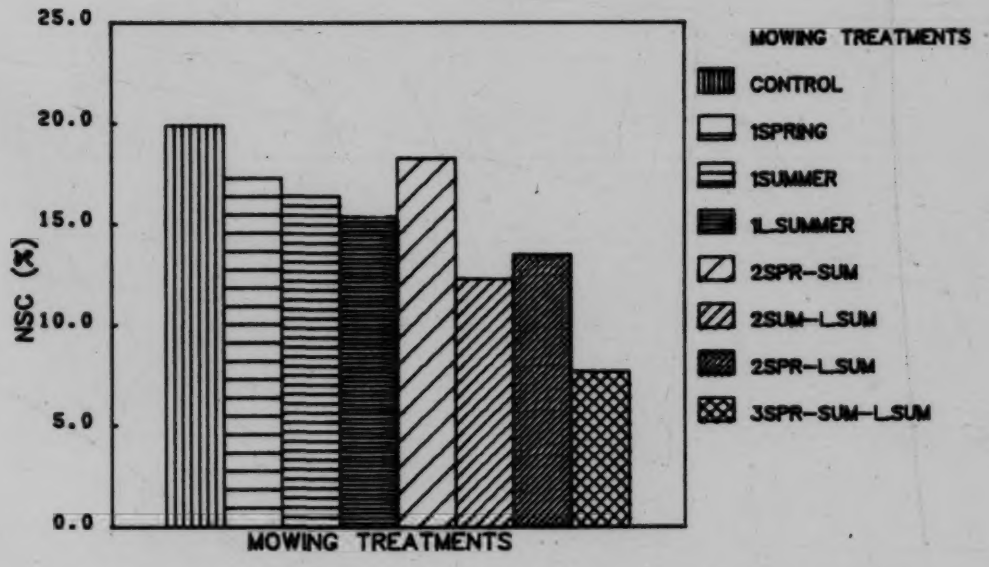

Fig. 21. Effect of season and frequency of mowing on NSC (%) in western snowberry root crowns excavated October 27, 1981.

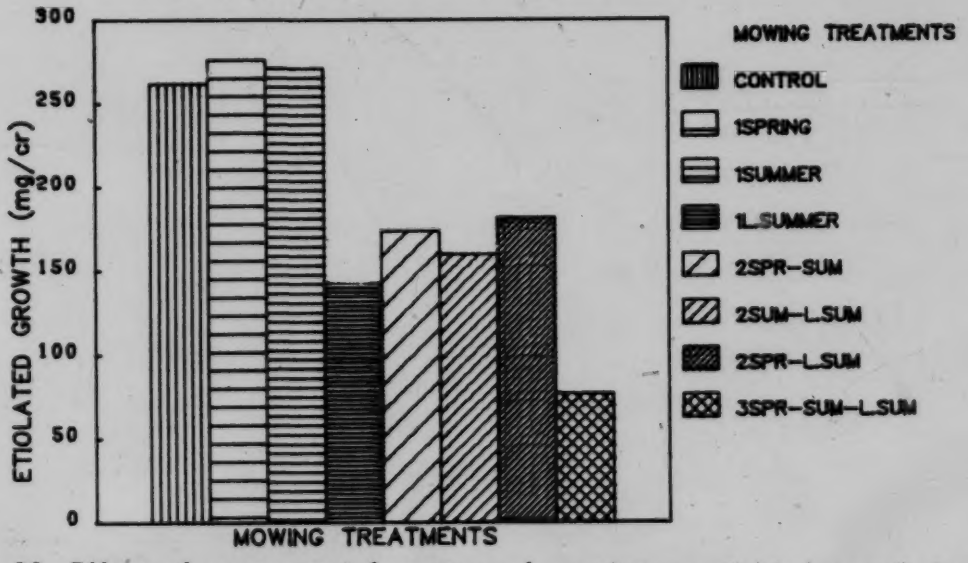

Fig. 22. Effect of season and frequency of mowing on etiolated growth (mg/cr) from western snowberry root crowns excavated October 27, 1981.

Table 10. Selected orthogonal comparisons[1] of the effect of season and frequency of mowing on nonstructural carbohydrate (NSC% by wt.) and etiolated growth (EG, mg/cr) in western snowberry root crowns, collected October 27, 1981.

	Control	Single Mow			Double Mow			Triple Mow		Parameters Tested[2]	
	unmowed	Spr.	Sum.	L. Sum.	Spr.-Sum.	Sum.-L. Sum.	Spr.-L. Sum.	Spr.-Sum.-L. Sum.	S. E.	NSC	EG
NSC	19.9	17.3	16.4	15.4	18.3	12.3	13.5	7.8	1.1		
EG	262	276	272	143	175	160	182	77	36		
1	+1	-1									
2	+1		-1							*	
3	+1			-1						*	*
4		+1	-1								
5		+1		-1							*
6			+1	-1							*
7					+1	-1				*	
8					+1		-1			*	
9						+1	-1				
10	+3	-1	-1	-1						*	
11		+1	+1	+1	-1	-1	-1				*
12					+1	+1	+1	-3		**	*
13		+1			-1						*
14		+1					-1			*	
15			+1			-1				*	*
16				+1		-1					
17					+1			-1		**	
18						+1		-1		**	
19							+1	-1		**	

1. Specific questions posed and the comparisons they refer to:
   a) Does season of cutting affect shrub yield? (Comparisons 1, 2 and 3)
   b) Do shrub yield reductions differ with varied season(s) of single and double cutting? (Comparisons 4 to 9)
   c) Does frequency of cutting affect shrub yield? (Comparisons 10, 11 and 12)
   d) Are added reductions in shrub yield derived from specific single versus double and double versus triple cutting sequences? (Comparisons 13 to 19)

2. Significant effects are indicated by * ($p < 0.05$, 24 d.f.) and ** ($p < 0.01$, 24 d.f.)

Major differences in the two reserve measures should be pointed out though. The substantial reduction with late cutting versus none with spring or summer cutting indicated an "all-or-none" type of response (Fig. 22 and Table 10).

Whereas season of cutting was important beyond the single cut treatments in NSC reserves, there were no significant differences (Table 10) in EG between the three double cut combinations (C 8, 9 and 10).

Increased frequency of cutting produced significant additional reductions, in autumn EG levels, with single versus double and double versus triple cutting (C 11 and 12). Although the increased frequency of cutting produced added reductions in yield, the progressive trend with late cutting was not apparent (Fig. 22). The effect of late season cutting was identified in the single late summer cut alone.

4.3.2 Discussion

Seasonal variation in NSC reserve levels reflects the unique phenology of each plant species (Moser 1977). Contrary to the results of Willard and McKell (1978), changes in the NSC status of western snowberry were evident in all tissue types that were analyzed. And further, the seasonal low corresponded with the stage of 2/3 shoot elongation rather than leaf flush. Much can be surmised from the comparison of seasonal NSC patterns in different plant components (Kramer and Kozlowski 1979). In particular, direction of flow may be inferred, and major sinks identified as storage sites adjacent to zones of carbohydrate utilization tend to show changes in NSC before those more distant.

It appeared that most demand for carbon was in aerial plant parts until after fruit swelling. Both of the initial phases of drawdown in the root zone were countered by increases in stem concentrations. Furthermore, these apparent phases of carbon movement from the roots to the stem corresponded with major developmental stages requiring carbohydrate, namely shoot elongation and fruit filling. Carbohydrate demand for fruit swelling did not persist past mid-August since stem NSC levels remained unchanged from this time onward, even after leaf senescence.

Root growth was not specifically monitored. However the contrast of slow recharge in the large root fraction with rapid initial recharge and then slow depletion in the root crown, may be indirect evidence of late season root growth. August and September may be the major period of root growth in many temperate woody plants (Taylor and Dumbroff 1975, Phillips *et al*. 1980). Although it has not been verified at this latitude in Alberta, Engle (1978) reported a late season decline in root reserves in gambel oak, in Colorado, and attributed it to late season root growth.

The early August decline in root crown NSC might also be related to rhizome growth since these structures arise directly from the storage organ in question. A low grade demand seems more likely since a commensurately large increment in rhizome length was not evident during the second drawdown period.

Growth and development priorities appeared to be altered in mowed clones as compared to unmowed ones. Reproductive activities, namely fruit production and rhizome extension, were reduced in favour of vegetative growth. This may have occurred to facilitate the re-establishment of adequate photosynthetic area. Compensatory regeneration is evident in the "free" growth pattern of the regenerating stands in which two flushes of shoot growth were produced, as compared to the "fixed" growth pattern observed in control clones, where only a single wave of shoot production occurred. In the spring-mowed clones, the sharp dip in NSC reserves observed during early August in control clones, was absent. The fact that fruit production was dramatically reduced in the spring mowed clones, supports the contention that the early August dip in the NSC cycle of control clones is related to fruit production. A hormonal imbalance likely resulted with spring mowing. If cytokinin production was reduced, a reduction in fruit filling would be one possible result (Kramer and Kozlowski 1979). This would further imply that fruit-sink demand would be reduced and carbohydrate would have been left in the roots. The net result was the re-establishment of spring NSC reserve levels when 40% of the original stand height had been regained about nine weeks after sucker initiation commenced.

Most shrub defoliation studies have treatments aimed at the simulation of browsing. These treatments tend to remove such a small proportion of leaf and stem material, that NSC reserve levels at the end of the growing season may remain unaffected (Willard and McKell 1978). In this study, repeated top removal produced significant reductions in dormant season NSC levels. The effect of season and frequency of defoliation on autumn NSC levels is consistent with the findings of Donart and Cook (1970). Treatment effect, measured here as fall NSC reserves, will depend on the time available for regrowth and replenishment. Spring mowing did not produce a reduction in fall NSC. Adequate time (i.e. > 60 days) and moisture were available to produce new growth and then to replenish root crown reserves. With progressively later cutting, significant reductions in autumn NSC reserves were detected. The summer cut also had adequate time for replenishment, but not as much as the spring cut. The late summer cut was timed during the major phase of late season recharge, during dormancy induction when reserves would be expected to be at or near the seasonal peak. The significant reduction in NSC, in the late-summer cut, may reflect slight use of reserves in the release of sprouts, late in the season.

The importance of late season recharge may account for the differences in fall reserves between the spring-summer double cut and the other three multiple cutting treatments. Recovery was apparent in the former while in the latter, reserves were depleted to varying degrees. A reduced growth flush after the June 24 cut, relative to that which followed the May 8 cut, might in fact be a response to day length. A reduced growth response would promote greater storage of current photosynthate and hence explain the recovery evident in the spring-summer double cut. Fall NSC was depleted in all other treatments. Late cutting likely interrupted the critical recharge phase. Assuming that the duration of drawdown was on the order of six to seven weeks, then snowberry plants in the summer-late summer and triple-mowed treatments would have just been entering the recharge phase when the last cutting occurred. Similarly, the ranking of the spring-late summer cut intermediate to the other double cuts may be related the fact that

there were an additional 50 days available for recharge than in the summer–late summer cut.

NSC and EG are common measures of reserve potential and tend to be correlated. NSC is a chemical measure while etiolated growth is an organic index. A number of researchers[23] regard EG as a more realistic measure of sprouting reserves than NSC (Klebasadel 1971). As a concrete measure of tissue expression, EG will account for possible differences in hormone levels and the developmental status of buds in addition to NSC reserves. In several studies reviewed by Menke (1973), accounting for the status of vegetative buds was important in the assessment of regrowth potential. Given equal NSC levels, outgrowth was directly related to the number of intact tillers of *Paspalum dilatatum* Poir. Similarly regrowth from *Agropyron repens* L. was a function of NSC and the number of intact dormant buds.

Of the three single cut treatments, the late–summer cut significantly reduced EG by an amount disproportional to the reduction in NSC. When compared to the summer cut, late–summer cutting reduced NSC by 5% of the total (1% NSC). However, EG was reduced by 50% by late–summer cutting as compared to the summer cut. This discrepancy may be related to bud condition. Frost or desiccation injury killed a sizeable proportion of late released sprouts. It therefore seems reasonable to conclude that late cut clones did not have the same supply of suppressed buds from which to produce new sprouts. Thus dark grown sprouts would be produced from buds of lower developmental status, possibly of adventitious origin. Based on the literature reviewed earlier (Thorpe and Murashige 1970), a higher energy cost may have been incurred in initiating sprouts from buds of lower developmental status. The net result was the outgrowth of only half the sprouts produced by spring or summer cut treatments, from roughly the same amount of stored NSC.

Differences in bud condition between treatments might have contributed further to contrasts between autumn NSC and EG profiles, but observations were not of sufficient detail to provide any meaningful insights.

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[23]McKenzie, J.S., personal communication, 1982. Canada Agriculture, Beaverlodge, Alberta.

The correlation of NSC with EG and the value of these indices in predicting regrowth yields will be discussed in the next section.

4.4 Effect of Treatment on Snowberry Regeneration

4.4.1 Results

4.4.1.1 Statistical Analysis

The orthogonal comparison procedure used in the previous section was employed in testing treatment effect on various stand parameters derived from estimates made in mid-August, 1982. Orthogonal comparisons were made for total annual yield and fruit yield of western snowberry, herbage yield, stem and plant density of snowberry. Grass and forb fractions were combined and analysed as total herbage yield since forbs accounted for less than 20% of total herbage. As in the previous section, the designated valid error mean square used in testing the sum of squares for each orthogonal contrast was CLONES within TREATMENT.

A stepwise multiple regression package[24] was used to assess the factors affecting total annual yield and stem density in 1982 in control and regenerating snowberry clones. Simple or multivariate linear regression equations were fitted by the method of least squares. Factor inclusion into each equation was at the $p<0.05$ level of significance. Independent variables considered in the yield regression included clone means for the following factors: (a) depth to clay, (b) distance to wetland, (c) age of the oldest root crown, (d) average clone age and, estimates made in the autumn of 1981 of (e) NSC, (f) EG and (g) residual stem weight. Residual stem weight is defined here as an estimate of the weight of stems and shoots, measured in the autumn of the year of treatment. This was the above ground weight of stems from which new growth would resume the following spring. Where only stubble remained, the value of residual stem weight was considered to be zero. In the stem

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[24]SPSS-Version H, Release 9, Feb. 1, 1982 - NEW REGRESSION.

density regression, all of the previous factors were included in addition to (h) frequency of cutting and (i) estimated soil temperature at the time of sucker initiation. Soil temperature values were extrapolated from Fig. 6 and 7.

Data from the Frog Lake study were analysed with a one way analysis of variance followed by testing of treatment means with a Student-Newman-Keuls test.

4.4.1.2 Effect of Treatment on Western Snowberry Yield in 1982

Total annual yield and fruit yield of western snowberry responded similarly to the season and frequency of cutting (Fig. 23). The results of orthogonal contrast testing for the two components were identical, though the magnitude of significance was higher for annual yield (Table 11). Single cutting caused substantial yield reductions relative to the control (C 1, 2 and 3). Summer and late-summer cuts yielded significantly less than did the spring cut (C 4, 5 and 6). Yield reductions did not differ significantly with varied seasons of double cutting (C 7, 8 and 9). Nonetheless, the magnitude of differences in fruit yield between double cuts may be of biological importance. Mean fruit yield for the spring-summer cut was ten-fold higher than the summer-late summer and twice that of the spring-late summer cut.

When the average effect of cutting frequency was considered, single and double cutting produced significant yield reductions for both total annual yield and fruit yield (C 10 and 11). The average reduction with triple cutting, beyond that produced by double cutting, was not signigicant (C 12). Significant added reductions were produced from an initial spring cut followed by summer or late-summer cutting (C 13 and 14). In short, season of cutting was important in the single cuts but beyond this, frequency was the main factor relating to further yield reductions.

In the first stepwise regression procedure (Table 12), the variability in Residual Stem Weight explained 82% of the variation in total annual shrub yield with EG reserves and mean Clone Age explaining an additional 4.9% and 1.8% respectively. Residual Stem Weight explained 67.5% of the variation in fruit yield; no other variables were included in the fruit yield regression. Curiously NSC reserves were

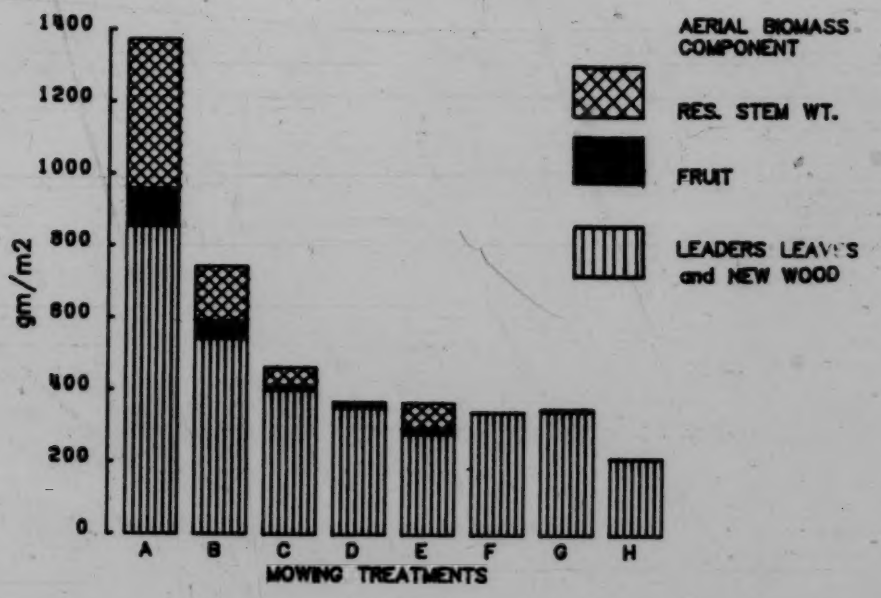

Fig. 23. Components of western snowberry total aerial biomass (gm/m²), sampled from control and treatment clones in mid-August 1982.

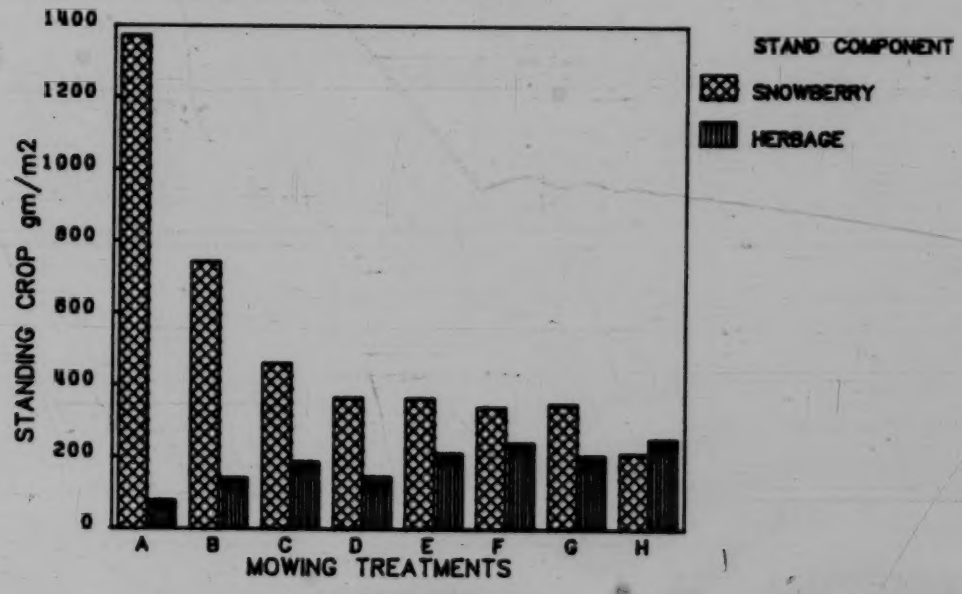

Fig. 24. Components of total aerial biomass (gm/m²) sampled from control and treatment clones of western snowberry in mid-August, 1982.

Table 11. Selected orthogonal comparisons[1] of the effect of season and frequency of mowing on yield (g/m^2) of snowberry and herbage in control and regenerating western snowberry clones as sampled in mid-August, 1982.

	Control	Single Mow			Double Mow			Triple Mow		Parameters Tested[2]		
	unmowed	Spr.	Sum.	L. Sum.	Spr.-Sum.	Sum.-L. Sum.	Spr.-L. Sum.	Spr.-Sum.-L. Sum.	S. E.	A Snowberry T. Ann. Yield	B Snowberry Fruit Yield	C Herbage Yield
A	960	592	414	367	294	341	350	213	50			
B	105	51	14	15	15	1	6	3	12			
C	79	141	186	146	212	241	206	251	15			
1	+1	-1								**	**	**
2	+1		-1							**	**	**
3	+1			-1						**	**	**
4		+1	-1							*	*	*
5		+1		-1						**	*	
6			+1	-1								
7					+1	-1						
8					+1		-1					
9						+1	-1					
10	+3	-1	-1	-1						**	**	**
11		+1	+1	+1	-1	-1	-1			**	*	**
12					+1	+1	+1	-3				
13		+1			-1					**	*	**
14		+1					-1			**	*	**
15			+1			-1						**
16				+1		-1						**
17					+1			-1				
18						+1		-1				
19							+1	-1				*

1. Specific questions posed and the comparisons they refer to:
   a) Does season of cutting affect shrub yield? (Comparisons 1, 2 and 3)
   b) Do shrub yield reductions differ with varied season(s) of single and double cutting? (Comparisons 4 to 9)
   c) Does frequency of cutting affect shrub yield? (Comparisons 10, 11 and 12)
   d) Are added reductions in shrub yield derived from specific single versus double and double versus triple cutting sequences? (Comparisons 13 to 19)
2. Significant effects are indicated by * ($p<0.05$, 24 d.f.) and ** ($p<0.01$, 24 d.f.)

Table 12. Regression analysis of factors affecting total annual and fruit yield (g/m^2) as sampled in control and regenerating snowberry clones in mid-August, 1982.

Parameter		Regression Coefficients	r^2	Change in r^2	S.E.E.[£]	Sig. of F[†]
TOTAL ANNUAL YIELD						**
Intercept	b0	427.81			117.42	
Res. St. Wt[‡]	b1	1.38	.820	+.820	.12	
Etiolated Reserves	b2	.61	.869	+.049	.19	
Clone Age	b3	-29.50	.887	+.018	14.14	
FRUIT YIELD						**
Intercept	b0	6.75			4.78	
Res. St. Wt.	b1	.23	.675	+.675	.02	

[£]Standard error of the estimate.
[†]** ($p<0.01$, 24 d.f.).
[‡]Residual Stem Weight

not included in either regression equation. Though NSC reserves were significantly and positively correlated with total annual yield (r=0.48), the simple correlations of residual stem weight and EG reserves to total annual yield were higher at r=0.91 and r=0.62, respectively. NSC and EG reserve estimates shared a surprisingly low, though significant simple correlation (r=0.43).

4.4.1.3 Effect of Treatment on Herbage Yield in 1982

Significant increases in herbage yield resulted from mowing (Fig. 24, Table 11). All single mowing treatments significantly increased forage production over the control (C 1, 2 and 3). Frequency of cutting (C 10, 11 and 12) appeared to be more important in increasing herbage yields than was season of cutting (C 4, 5, 6, 7, 8, and 9). All added effects comparisons showed significant increases over single cuts (C 13, 14, 15 and 16), regardless of cutting dates.

4.4.1.4 Effect of Treatment on Stand Structure in 1982

Treatment not only altered snowberry and herbage yield, but also changed shrub stand structure. Plant numbers are difficult to assess in woody plants such as snowberry where root crowns tend to be connected by underground rhizomes. A minimum distance requirement of 5 cm, measured at soil surface, was used in estimating plant numbers in each quadrat. Most snowberry stems arise in clusters from distinct root crowns. With this sampling approach single sprouts or crown clusters would be counted as individual plants, the intent being to assess the relative number of sources of stem growth between treatments and give an indication of overall net change.

A single spring cut (C 1) and double cutting in general (C 11), significantly increased plant numbers relative to the control (Table 13).

Season of cutting affected stem density in double cut treatments. Significant increases were derived in double cuts with spring–late summer and summer–late summer cuts (C 14, 15 and 16).

Table 13. Selected orthogonal comparisons[1] of the effect of season and frequency of mowing on plant and stem density in control and regenerating western snowberry clones as sampled in mid-August, 1982.

	Control	Single Mow			Double Mow			Triple Mow		Parameters Tested[2]	
	unmowed	Spr.	Sum.	L. Sum.	Spr.-Sum.	Sum.-L. Sum.	Spr.-L. Sum.	Spr.-Sum.-L. Sum.	S. E.	A Plants/m^2	B Stems/m^2
A	31.3	44.0	39.2	32.4	43.4	44.8	47.1	37.3	3.4		
B	75	138	113	113	134	232	243	170	28		
1	+1	-1								*	
2	+1		-1								
3	+1			-1							
4		+1	-1								
5		+1		-1						*	
6			+1	-1							
7					+1	-1					*
8					+1		-1				*
9						+1	-1				
10	+3	-1	-1	-1							
11		+1	+1	+1	-1	-1	-1			*	*
12					+1	+1	+1	-3			
13		+1			-1						
14		+1					-1				*
15			+1			-1					**
16				+1		-1				*	**
17					+1			-1			
18						+1		-1			
19							+1	-1			

1. Specific questions posed and the comparisons they refer to:
   a) Does season of cutting affect shrub yield? (Comparisons 1, 2 and 3)
   b) Do shrub yield reductions differ with varied season(s) of single and double cutting? (Comparisons 4 to 9)
   c) Does frequency of cutting affect shrub yield? (Comparisons 10, 11 and 12)
   d) Are added reductions in shrub yield derived from specific single versus double and double versus triple cutting sequences? (Comparisons 13 to 19)

2. Significant effects are indicated by * ($p < 0.05$, 24 d.f.) and ** ($p < 0.01$, 24 d.f.)

Of the nine independent variables tested in the regression analysis, Frequency of Cutting was the only variable selected that explained a significant proportion of the variation in stem density (27%, F=11.3**).

4.4.1.5 Frog Lake Study

Western snowberry regrew slowly for the first two years after the late-summer (July 9, 1979) cutting. New sprouts were delayed until August of 1980, whereas spring cutting in 1982 was followed by immediate and vigorous sprouting. Precipitation records indicate that there was 310 mm of snow on the ground at the end of March, 1980 and that growing season precipitation totalled 270 mm, most of which fell from late May to August[25]. Precipitation was, therefore, not a factor limiting the regeneration of the late-summer cut during the following growing season.

At the time of plot sampling (August 28, 1982), western snowberry plants in the late-summer cut exhibited a dwarfed growth habit (Fig. 25a). Incremental growth produced during the previous two growing seasons ranged from 3 to 5 cm in length. After three years growth, overall plant height averaged 15 cm. In contrast, suckers produced in the spring of 1982 mowing had achieved substantial linear growth (25-30 cm) in a single season (Fig. 25b).

Comparison of treatment means for annual yield, old stem weight, standing crop and stem density of snowberry gave greater definition to the qualitative differences observed (Table 14). In three growing seasons, 20% of the shrub standing crop of the control was regained in the late-summer mowing treatment; most of this being produced in the 1982 growing season. In a single growing season, the spring cut regained 42% of the shrub standing crop of the control. Three years after treatment, stem density in the late-summer cut, remained significantly higher than the control and not substantially different from the 1982 spring mow.

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[25] Atmospheric Environment Service, Tulliby Lake weather station located 6 km east of the study site.

COLOURED PICTURES
Images en couleur

Fig. 25. A comparison of sprouting morphologies of snowberry stems from early (a) and late cut (b) stands.

Table 14. Western snowberry stand parameters[1], from plots harvested August 28, 1982 at Frog Lake.

	Treatments			
	Control	Late summer 1979	Spring-1982	S.E.
SNOWBERRY:				
Annual Yield (g/m²)	203b	70a	199b	21
Old Stem (g/m²)	272b	31a	–	26
T. Stand. Crop (g/m²)	475c	101a	199b	28
% of Control	100	21	42	
Stems/m²	87a	174b	144ab	21
Herbage (g/m²)	100a	148b	152b	15

[1]Means within rows, followed by the same letter, are not significantly different (Student–Newman–Keuls test, $p<0.05$).

4.4.2 Discussion

There was abundant regeneration of western snowberry after mowing in this study. Anderson and Bailey (1979) reported a similar response following spring burning. However when FitzGerald (1982) imposed early July grazing following May burning of a regenerating aspen forest, regrowth from western snowberry was delayed until the next spring. FitzGerald's results are not directly comparable to the present study since defoliation by grazing was not complete, probably due to low shrub palatability. Therefore some degree of apical dominance over vegetative buds may have been retained.

In the current study, the growth interval appeared to be limited by the the seasonal constraints of spring soil temperature and late-summer photoperiod. Although evidence is indirect, drought enforced dormancy did not appear to be a factor limiting growth in 1981 and 1982.

In the carbohydrate studies, the length of the growing season available after treatment seemed an important factor relating to recovery of autumn NSC reserves. Near complete recovery was evident in four of the treatments where recovery time was adequate. Therefore it is not surprising that regression analysis selected residual stem weight as the key factor predicting 1982 snowberry yield. The trend towards higher 1982 yields with greater residual stem weight is consistent with the findings of Humphreys and Robinson (1966) for tropical grasses. They found that when resources, especially moisture, are in adequate supply, growth is more dependent upon leaf area than NSC concentration. Although leaf area was not specifically measured, the assumption made here is that a greater stem weight would mean a greater leaf area.

EG was a better predictor of 1982 yields than was NSC, presumably because EG may account for the interaction of the developmental status of buds and chemical reserves. In the regression equation for total annual yield of snowberry, the variation in residual stem weight may have accounted, in part, for NSC and EG reserves. When residual stem weight was removed from the equation, EG accounted for 16% more of the variation in yield than did NSC, when EG was in turn removed (r^2=.38 for EG, F=18.7**; r^2=.22 for NSC, F=8.77**). It would appear that the value of EG reserves for predicting

the yields of other plants may also apply to western snowberry.

The variation in residual stem weight was the best predictor of total annual shrub yield and fruit yield in 1982. As the amount of overwintering stem material increased, the yield of annual growth and fruit, increased also. Yields reported for single cut treatments are closely related to this relationship. At the lower end of the trend line, triple cutting produced a predictable result. As in aspen poplar, repeated cutting with subsequent sprouting and outgrowth will eventually reduce stand vigour (Berry and Stiell 1978) likely through the depletion of NSC reserves (Tew 1970, Schier and Zasada 1973). However, when compared, the total annual shrub yields of double cut treatments are inconsistent with this relationship. Annual yields were in fact higher in the treatments that lacked overwintering stem material (F and G). This apparent disagreement may be explained by the interaction of phenology with precipitation patterns during the summer of 1982. Owing to the greater stem biomass at leafout in the spring-summer cut (E), flowering commenced 1 to 2 weeks earlier than in the other two treatments (F and G). Optimal rainfall in July (163 mm) promoted vegetative growth in treatments F and G while in treatment E, development advanced beyond the point where further vegetative growth could occur. In treatment E developmental priorities were likely shifted in favour of fruit production and would therefore account for the higher fruit yield in E than in F and G.

A total of 86.9% of the variation in 1982 yields was explained by independent variables directly related to treatment (i.e., residual stem weight and EG). Variation in yield explained by environmental factors was negligible. Possible physiological reasons for the decline in clone yield with increasing age are unclear. Pelton (1953) failed to detect any symptoms of decline or senescence in the oldest snowberry clones examined in his study; some were three times older than those sampled in this study.

In mowed clones, release from apical dominance accounted for the increase in plant and stem density. Stem density increased two to three fold. These values are lower than the post burn increases of three to five fold reported by Anderson and Bailey (1979). The interaction of soil temperature and frequency of cutting appears to explain the stem densities recorded in my study. In single cut treatments, apical dominance was quickly

reestablished with the most advanced shoots asserting control over those of lower developmental status. Re-cutting released vegetative buds, once again, from apical dominance. The sizeable increase in stem density in double cut treatments may be related to soil temperature. The independent variable, soil temperature, was not included in the stepwise regression but was likely confounded with frequency since the simple correlation of these two variables was quite high (r=.82). When frequency was removed from the equation, temperature ranked first among the remaining variables and accounted for 21% of the variation in stem density (F=7.9**). Though post burn soil temperatures were not specifically monitored by Anderson and Bailey (1979), a blackened and exposed soil surface may have promoted much higher soil temperatures during sprouting than were recorded in this study. Consequently, much higher stem densities resulted from a single spring burn as compared to a spring mow, presumably due to the influence of higher soil temperatures on auxin destruction (Schier 1976).

In this study, late mowing in multiple cut treatments, would have further arrested the re-establishment of apical dominance. This combined with the natural trend over the growing season towards warming of the soil surface, and an added increase due to ground exposure from repeated cutting, seems to account for the higher stem densities relative to other treatments. The change in plant density is probably related to the same factors.

The apparent decline in stem and plant density in summer and late-summer single cuts relative to the spring cut, seems to contradict the explanation offered above. However, given that both the former treatments produced sprouts during the late season, frost injury may have had a thinning effect on the resulting stand. Though sprout mortality was observed solely in the single late summer cut, it is possible that sprouts produced during late July, in the summer cut, were also injured but went undetected due to their more advanced developmental status.

The relevance of the Frog Lake study will be discussed in the next chapter.

5. Summary and Management Implications

The principal study site at Beaverhill Lake may be considered somewhat atypical for the aspen parkland. A higher soil moisture regime and heavier stand type were found here as compared to those described by Wroe (1971) and Wheeler (1976). However, the site in question was favoured for a number of reasons. Aside from the abundance of individual snowberry clones from which a uniform treatment population could be selected, soil moisture, the environmental variable most often limiting regrowth of woody plants (Lavender 1980), was not a limiting factor. Consequently sprouting behavior of western snowberry, in relation to the treatments imposed, could be monitored under optimum field conditions, making extrapolation of physiological findings to environments of greater soil moisture stress, a more logical approach than vice-versa.

A number of competitive adaptations of western snowberry may be surmised from the soil temperature and soil moisture conditions documented in this study. Higher soil temperatures and lower soil moisture levels in the grassland than in the shrubland, may set up the initial environmental stimuli for clonal expansion by rhizomes (Schier 1976). Findings reported here indicate that once established, western snowberry acts as wind breaking vegetation, altering snow deposition patterns at the expense of adjacent vegetation types. Greater snow pack improves soil moisture supply thereby promoting vigorous growth and buffering against drought (Daubenmire 1974). Stoeckeler and Dortignac (1941) reported greater shelterbelt longevity where "snow fence" vegetation trapped snow and improved the supply of soil moisture. Furthermore, greater snow pack serves to reduce the severity of winter soil temperatures. From this it may be argued that late mowing may reduce the competitive advantage of snowberry over other species. However, in this study, the short term changes resulting from late mowing seem of questionable biological significance. With site types of a more xeric nature, such as at Frog Lake, the effects of late mowing may be greater.

FitzGerald (1982) felt that control of aspen by repeated defoliation would be laborious and expensive. Aspen root reserves were sufficient to feed numerous sucker crops. He concluded that further investigation of the causes of control with August

grazing was apt to be more rewarding. Under the regime of cutting and environmental conditions present at the Beaverhill Lake site, western snowberry was reduced as a stand component but by no means eliminated. In the initial stages of the study, maximized depletion of NSC reserves in snowberry seemed a logical approach to achieving the greatest degree of physiological stress. Although the initial spring cutting date occurred prior to the spring NSC low in the control clones (at 2/3 shoot elongation), reserves were nonetheless depleted to 35% of the control by triple cutting. In spite of this major reduction in root crown NSC, triple mowed clones, which exhibited the greatest reduction in vigour, produced 2135 kg/ha of total aerial biomass of snowberry in 1982. Though stand composition was temporarily shifted in favour of herbage (2513 kg/ha), the vigour and density of snowberry regrowth produced in 1982, would ensure the re-establishment of shrub dominance in the foreseeable future. A snowberry plot located outside of the main study area received as many as five mowing treatments within a 2 year period. Though vigor was obviously reduced, abundant sprouting was evident at the end of the second year.

Western snowberry is particularly well adapted to spring or summer cutting regimes. These results show that by the time an average of eleven leaf pairs have been produced, recharge of root NSC reserves will commence. In 1981 this was nine weeks after spring mowing (at the leafout stage) and six to seven weeks after the first new sprouts were observed. Duration of recharge was approximately 3 weeks with anthesis in the new sprouts signaling recovery to spring NSC reserve levels.

A further adaptation lies in the manner in which each subsequent wave of sprouts was produced. After spring or summer cutting, new stems appeared from what Schier (1981) described in aspen as currently initiated buds. After the first decapitation, new sprouts originated from axillary buds closest to the cut surface. When second and third cuts were applied, each subsequent wave of sprouts arose from currently initiated buds just above the base of the previous sprout. In this way, suppressed buds located in positions subtending the first wave sprouts, were kept in reserve.

The effect of different season and frequency of mowing, as evaluated from snowberry yield, indicated that production of new growth in 1982 was primarily related to the amount of regrowth produced and allowed to overwinter in 1981. A further ranking of yields, from treatments that regenerated from ground level, should have been comparable to differences in NSC levels measured in the fall of 1981. The triple cut was the only mowing treatment, regenerating from ground level in 1982, in which the ranking of shrub yield relative to other treatments, was comparable to the ranking of fall NSC reserves. Annual yield in the summer-late summer and spring-late summer ranked higher than the spring-summer cut. This result was inconsistent with the overall trend of higher 1982 shrub yield with more overwintering stem material. A possible explanation for this may lie in the interaction of phenology with precipitation patterns, as described in the last chapter.

FitzGerald (1982) felt that late grazing may have interrupted the normal induction of dormancy in aspen resulting in frost injury and reduced regeneration. Late-summer cutting at Beaverhill Lake did not produce the same dramatic effect in snowberry. The winter of 1981-82 was an ideal one for frost injury if mowing had effected a general reduction in the level of tissue hardiness. Not only were temperatures extreme and the winter of long duration but soil temperature fluctuations were greater in mowed stands. Somers (1981) pointed out that in high arctic shrubs, temperature appears to substitute for daylength in the induction of winter hardiness. Although exposure of high arctic shrubs in the laboratory to far red light and short days, produced greater cold hardiness, Somers concluded that in the field, endogenous factors sensitive to low temperatures (+5 to -5°C) were most important in eliciting the changes necessary for winter survival. Even if mowing did alter the initial stages of dormancy induction, normally associated with daylength and light quality, there is good evidence (Somers 1980) that temperature may substitute in promotion of frost hardiness.

Bud phenology, in relation to the season of cutting is of key importance in this study. It is pertinent to note that the production of late season or "Lammas day" shoots has been reported for a number of temperate woody plants (Kozlowski 1971a). They are

so named because of their tendency to occur around August 1. These sprouts tend to be released during the period of transition between strong apical control over lateral buds to the late season period of general bud dormancy. In western snowberry, the mid-summer growth pattern of rhizomes, the timing of rebranching (in regenerating stands), and the gradient in bud release with progressively later cutting dates, appear to correspond to this transition phase. Furthermore, these late shoots may render trees more susceptible to frost injury (Kramer and Kozlowski 1979).

In grape culture, primary buds released at basal nodes, following late summer pruning, are highly susceptible to desiccation or frost injury (Howell and Wolpert 1978). In temperate zone viticulture a five stage classification by Baggiolini (Howell and Wolpert 1978) is routinely used to estimate primary bud vulnerability to frost damage and includes the following stages: (a) dormant (b) scale crack (c) swell 1 (d) swell 2 and (e) burst. Up until the second stage of bud swelling, bud hardiness remains comparatively high for such a sensitive species (i.e. -15 to -4.5°C). As soon as apical burst initiates though, frost resistance is completely lost. Yield reductions from primary bud injury may be so extreme that special pruning procedures are required to delay bud release or else remove damaged canes just prior to the normal growth period. The presence of frost-damaged buds in grapes tends to reduce the productivity of secondaries.

Severe winter injury to native deciduous species has also been linked to bud phenology. Cayford *et al*. (1959) reported that in Saskatchewan and Manitoba, during the winter of 1957-58, premature bud break was initiated by warm winds in late winter. Injury from April frosts was directly proportional to the degree of bud burst and chlorophyll development. Many trees suffered winter injury to a high proportion of their vegetative buds.

The actual mode of injury may, in fact, be the result of desiccation rather than intracellular ice formation. The progression of vegetative buds to the bud burst stage implies that stomata on primordial leaves become active at the time when normal water relations in the plant have been altered for the winter (i.e. suberized roots or frozen soil preventing water uptake) and desiccation therefore results (Kozlowski 1971a).

Injury of primary vegetative buds in woody plants can drastically alter the developmental morphology of new growth (Smith and Olien 1981). Where severe depletion of the pool of primary vegetative buds has occurred, the subsequent outgrowth of new shoots is delayed, often till late in the season, and is characterized by the production of adventitious or short shoots (Cayford *et al*. 1959, Egeberg 1963, Smith and Olien 1981). New shoots often exhibit a peculiar stunted growth with bushy and prostrate morphologies, resembling arctic species (Smith and Olien 1981).

When the results of early and late cutting at the two different locations are compared, the net result of treatment appears superficially quite different. However, in light of the limited investigation by Pelton (1953), similar treatment effects may have occurred. The differences between sites in subsequent shrub stands may have been influenced by cutting date and soil moisture regime. At Beaverhill Lake, mowing during the first two weeks of August resulted in the release of late season sprouts. Winter injury was evident in approximately 30% of the released buds, most of which arose from axillary positions. Bud release diminished with progressively later cutting dates. Buds that failed to break the surface remained viable. In the late cut, a change in sprouting morphology was reflected in the significantly higher proportion of new sprouts in 1982 arising from basal rather than axillary positions. In contrast new sprouts arising in all other mowing treatments were initiated from suppressed buds or buds emerging after spring or summer cuts (termed "currently initiated"). Furthermore, two important results described for the single late cut imply that new shoots developed from buds of lower developmental status. Firstly, EG reserves were disproportionally lower than were NSC levels and secondly sprout initiation was of prolonged duration. This was interpreted to indicate that a portion of the dormant buds of high developmental status were depleted because of late cutting leading to frost injury. A higher energy cost and longer duration of sucker initiation would be expected as buds of lower developmental status were activated.

On the drier Frog Lake site one can only speculate as to the actual processes involved in producing the dwarfed stand in the late cut versus the more vigorous one in the early cut. Given the basic response outlined for the late cut on the Beaverhill Lake site and

the apparent overriding control of daylength on bud dormancy, it seems reasonable to infer that the July 29, 1979 cutting resulted in a higher level of bud injury. By cutting on an earlier date, dormant buds released from the stump would have elongated to a greater extent than if cut one or two weeks later. Given the relationship of bud burst to desiccation injury, a greater percentage of injured buds may have resulted. If the principal source of new sprouts was from adventitious buds, this would further explain the delay in regeneration, the short shoot increments in each subsequent year and the generally dwarfed plants compared to the robust ones evident after spring cutting.

The extent of bud injury and the ability of the plant to produce new buds will be influenced by soil moisture regime. The actual degree of bud injury may be reduced on sites where high soil moisture levels help buffer changes in soil temperature (Howell and Dennis 1981). Moisture stress during bud development may limit ultimate developmental and outgrowth potential of the new shoot (Zahner 1968). The more favourable soil moisture conditions on the Beaverhill Lake site may, therefore, relate to the lesser effect due to late cutting.

Yield was not as severely affected by late cutting on the moist site as on the dry one. Although plant and stem densities were apparently reduced by frost action, nevertheless, vigorous growth was produced from surviving stump buds and from meristems that differentiated in the spring of 1982. Apical dominance in the late cut was, therefore, re-established in short order at Beaverhill Lake. Final stem and plant densities, were not significantly different from the control. Curiously, at the Frog Lake site, stem density in the late cut remained double that of the control three years after treatment. Anderson and Bailey (1979) reported a progressive decline in stem density by the third year after spring burning, as certain stems reestablished dominance over subordinate stems. At Frog Lake, the low yield, high stem density and dwarfed nature of snowberry indicated a prolonged competition between plants, without the clear re-establishment of apical dominance.

A number of parallels may be drawn between the effect of late cutting on western snowberry and the response of certain alfalfa cultivars to late summer harvest. McKenzie

and McLean (1980b) have observed a similar late season release of frost susceptible sprouts in alfalfa with August cutting. As with snowberry, injury is correlated with sprout emergence and green tip development.[26] In alfalfa, the late release of sprouts implies the return to a state of vulnerability to winter injury. Yield and stand reductions may result in subsequent years. Consequently, McKenzie and McLean (1980a) recommended that cutting during August be avoided.

Western snowberry exhibited a strong periodicity or link to photoperiod in its sprouting response. Though climatic conditions differed substantially between years, sprouting response displayed the same daylength related decline with progressively later cutting dates. Siminovitch (1981) has reported that herbaceous plants are influenced far more by environmental variation than are woody plants. In alfalfa, high soil moisture levels, in autumn, may lead to a similar return to a tender vulnerable state as might late harvest. However, it seems that in snowberry, high soil moisture levels did not delay or enhance sprout release.

It is clear that although mowing may temporarily reduce snowberry yields, and possibly to a much greater extent on drier sites, mowing by itself is not an effective control treatment. However, these findings point to the potential to improve the effectiveness of 2,4-D ester applications as follow up treatments in the control of western snowberry. The killing of root buds in woody plants with phenoxy herbicides depends on downward movement of the herbicide in the translocation stream (Muzik 1970, Moser 1977), which in turn is influenced by root sink strength (Fick and Sosebee 1981). Many workers have correlated the best kill of basal buds with the major period of root recharge (Hyder *et al*. 1969, Boo and Petit 1975, Fick and Sosebee 1981). However, it is not sufficient to solely define periods of root recharge. Leaf maturity may limit herbicide penetration. Fick and Sosebee (1981) obtained high levels of root bud kill with spray applications to honey mesquite during the early season root recharge phase. During the late recharge though, leaf maturity limited herbicide penetration. The seasonal NSC cycle defined for western snowberry in this study would indicate that herbicide be applied

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[26]McKenzie, J.S. 1982. Personal communication. Canada Agriculture, Beaverlodge, Alberta

just past the peak phase of shoot elongation in mature snowberry stands. However leaf maturity is repeatedly cited as a factor limiting herbicide penetration in this shrub (Friesen *et al*. 1965). Good top kills may be obtained by applications during leaf expansion but most translocation is acropetal at this stage. By the time basipetal recharge begins, leaves become leathery and resistant to herbicide.

Top removal, be it by mowing or burning and regardless of the season, provides the opportunity of initiating a new wave of regrowth which will deplete root reserves to a much greater extent than would occur in unmowed stands. This would further facilitate a shrub canopy of more vegetative character during the phase of root recharge. These physiological responses, have been related to enhanced herbicidal control of red maple (Upchurch *et al*. 1969) and honey mesquite (Beck *et al*. 1975). In this study, snowberry sprouts retained a tender green appearance up to the time of root recharge. Beck *et al*. (1975) speculated that a similar vegetative condition in honey mesquite stems may have fostered direct herbicide penetration into the phloem tissue when root recharge was underway thus resulting in a high level of root kill.

Furthermore, it may be possible to deplete the supply of suppressed buds and alter shoot morphology with late-summer cutting. Although shoot morphology was not specifically characterized at the main study site, evidence has been presented that new shoots may have been produced from vegetative buds of lower developmental status and possibly of adventitious origin. At the Frog Lake site where a more dramatic treatment effect was documented, regrowth in the late cut conformed to the morphology expected when shoots are produced from adventitious buds; namely of a stunted and dwarfed nature and largely lacking flowers and fruit.

Shoots displaying a limited growth potential and lacking flower buds or secondary vegetative buds are termed "short shoots" (Kozlowski 1971a, Zimmerman and Brown 1971, Dahl and Hyder 1977). A higher proportion of short shoots in regenerating deciduous species has practical value with herbicide follow up treatments (Dahl and Hyder 1977). Greater levels of control with phenoxy herbicides are associated with such stands (Wilson *et al*. 1975) since short shoots have a greater tendency to basipetal transport than

do long shoots (Dahl and Hyder 1977). Normal long shoots, which may be completely preformed in the bud, logically display greater apical sink strength associated with the needs of flowering and rebranching. A greater tendency to acropetal transport is therefore inherent.

The real potential to deplete the supply of suppressed buds thereby forcing new sprouts to arise from adventitious buds, appears to lie in maximizing the release of late season sprouts. These must be released at such a time that they will have adequate time and stimulation to elongate and break the soil surface yet not enough to completely leaf out and develop frost hardy apices. Further research is required to more clearly define this critical period and at regionally meaningful latitudes. The cutting dates employed here appeared to define the latter portion of this hypothesized "critical cutting" interval. A review of the literature indicates that ethylene[27], a plant growth regulator, may have potential to enhance the release of sprouts in late mowed clones of western snowberry. Morgan *et al.* (1969) employed ethephon applications to activate basal buds in seedlings of honey mesquite. In contrast, ethephon applied to mature honey mesquite plants reduced flower production but had no effect on basal sprouting (Parsons and Sosebee 1974). Excised aspen root sections, soaked in aqueous solutions containing ethephon at 100 mg/l, increased bud release by 50% of the control and also enhanced sprout elongation (Schier and Campbell 1978). Higher concentrations inhibited the release of aspen buds. Further research into the use of such a growth regulator, for the enhancement of sprout release in western snowberry, may be potentially rewarding.

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[27]Ethylene may be generated from ethephon [(2-chloroethyl phosphonic acid], an inexpensive and readily available source.

6. Conclusions

Major results and conclusions from the experiments were as follows:

1. In mature western snowberry plants, the first low in NSC reserves during the growing season coincided with the phenological stage of 2/3 shoot elongation, not with leafout as was previously suspected.

2. The second low in NSC reserves occurred during fruit swelling.

3. Spring mowing caused a greater and more prolonged reduction in NSC reserves than was evident in the control.

4. Western snowberry clones, mowed in the spring, were able to replenish NSC reserves in a single season. Root recharge commenced when new suckers had eleven leaf pairs. Stem maturation marked by a change in color from pale green to rusty brown, was evident in the latter part of the recharge phase. Root recharge was complete when flowering was observed.

5. The greatest reductions in autumn NSC reserves were obtained with late-summer cutting.

6. A significant reduction in sprouting reserves, measured from etiolated growth, resulted from late-summer cutting. This reduction was attributed to a higher energy cost incurred in releasing vegetative buds of lower developmental status, to replace buds, which emerged after late cutting and had been frost injured.

7. Season of mowing affected sprouting morphology. Spring and summer cutting favoured stump sprouting while cutting in the late-summer promoted sprouting from the root crown.

8. Sprout release was not apparent where cutting occurred beyond mid-August.

9. Late-summer cutting may result in greater reductions in vigour on dry sites than on moist sites.

10. Although increases in herbage production were substantial, mowing failed to control western snowberry on the Beaverhill Lake site where soil moisture was not limiting.

11. In the season following treatment, current shrub yield was related to the time available for regrowth after cutting, in 1981, and hence the amount of overwintering stem material from which new growth could arise.

12. When two measures of sprouting reserves were compared, etiolated growth was a better predictor of post-treatment shrub yields than was non-structural carbohydrate.

13. Soil temperature increased through the growing season, reaching a maximum in early August.

14. Mowing caused a further 1 to 4°C increase in soil temperature.

15. The greatest increases in stem and plant densities occurred in multiple cut treatments where late-summer cutting was included.

16. The elimination of shrub cover with late mowing caused a reduction in snow accumulation on mowed sites.

17. Winter soil temperatures fluctuated more and were lower for a longer duration in late-mowed clones as compared to unmowed ones.

18. Although late mowing appeared to result in a more severe winter environment and may also account for reduced soil moisture levels. during the season following treatment, these environmental changes were of questionable biological significance.

7. Recommendations

Based on the findings presented in this thesis and the literature reviewed, the following recommendations are tentatively put forward.

On open shrubland where surface stoniness and topography do not limit mowing, western snowberry should be mowed between July 15 and August 15 during the first year of treatment. New growth, produced the following spring, should be sprayed with a high rate and volume ground application of 2,4-D ester, when suckers are between the 11 leaf pair stage and flowering in their development. Apply 1.6 to 2.2 kg/ha of 2,4-D ester in 115 to 230 L/ha of water carrier.

On shrubland which may be subject to periodic drought, late mowing should be carried out in years when soil moisture is available, not in drought years. If a weak flush of sucker regrowth is evident, during the spring following late-summer mowing, then defer the herbicide followup treatment until the second growing season after mowing.

It must be acknowledged that control of western snowberry may be neither feasible nor economical on rangelands which are excessively stony or, which have rough topography. Prescribed burning may be a useful pretreatment where site factors limit mechanical operations. Spring burning should be followed by a herbicide application timed as mentioned in the first prescription. Aerial rather than ground spray application may be a further trade-off required because of site limitations.

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9. Appendices

9.1 Appendix 1 - Stand Characteristics of Control Clones

9.1.1 Results

9.1.1.1 Age Class and Biomass Distribution Between Root Crowns and Stems

The age class distribution of stems versus that of root crowns in control clones is depicted in Fig. 26. The difference in age class distribution between above and below ground components is striking. Few stems were older than 10 years, whereas root crowns of up to 25 years of age were present. Stem age was evenly distributed between the 1 to 5 and 6 to 10 year age classes, with only 4% of stems being older than 10 years. In root crowns, the 6-10 year class predominated, with 30% of crowns being older than 10 years. Mean stem age was 3.6 years while root crowns were twice as old at 7.8 years (Table 15). When the means for stems and root crowns were compared, root crowns were significantly older in all clones. While there were no significant differences in the age of stems among clones, the root crowns of clone number 4 were significantly younger than those of the other control clones.

The ratio of stem to root mass calculated for all of the control clones was 1:1.3.

9.1.1.2 Stem Class Distribution

Density of live and dead old stems as well as live and dead current sprouts, is presented in Table 8. On average about one quarter of the above ground stems were dead, 18% being old stems and 4% being current sprouts, while 69% were live old stems and 9% were live current sprouts.

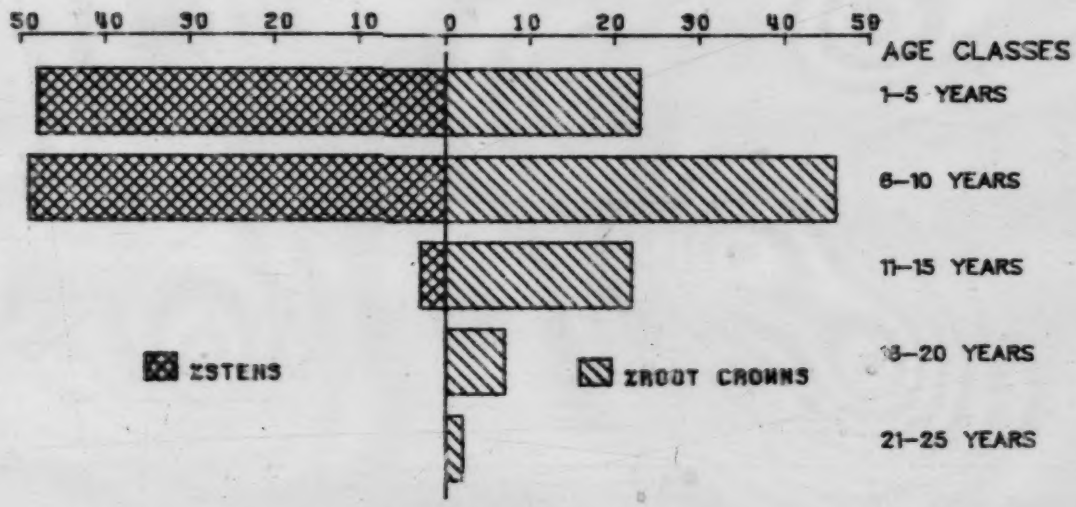

Fig. 26 Age class distribution of snowberry stems versus root crowns in four control clones (n=240 for root crowns and n=332 for stems).

Table 15. Age[1] of stems versus root crowns (yr) of western snowberry in control clones.

	Clone 1	Clone 2	Clone 3	Clone 4	Mean
n[2]	n=81	n=94	n=71	n=86	
Stem age	3.49b	3.38b	3.95b	3.90b	3.68
S.E.	.30	.18	.23	.20	
n	n=48	n=58	n=67	n=67	
Root crown	8.87a	7.46ab	8.46b	6.76b	7.88
S.E.	.79	.59	.49	.44	

[1]Means within rows followed by the same letter are not significantly different (student t test, $p<0.05$). All differences between means within columns were significant.
[2]Denotes the number of samples from which the mean was determined.

Table 16. Density of live and dead old stems[1] and live and dead current year sprouts (no./m²) in control clones in mid-August, 1982.

	Stem Class			
	Live Stems	Live Sprouts	Dead Stems	Dead Sprouts
Clone 1	64	7	12	1
Clone 2	79	10	11	2
Clone 3	56	9	20	3
Clone 4	68	8	26	12
Mean	66	9	17	4
S.E.	2.4	.9	1.7	.9
Mean %	69	9	18	4

[1]Includes all stems more than one year old.

In 1981, a powdery white material was observed at the base of current sprouts, particularly under dense shrub cover. The substance was later identified as a material produced by ground mealy bugs (*Pseudococcus spp.*),[23] an insect with piercing and sucking mouth parts and that rears its young in the woolly byproduct. The seasonal activity of the insects appeared to differ between years of the study. In 1981, the powdery white substance was visible on sprout bases, early in the season, prior to stem lignification. Black epidermal scarring and stem mortality were observed in conjunction with the substance. However, in 1982, the white material appeared after the heavy rains of July, after epidermal tissue on new sprouts had changed to the characteristic rusty brown color. The stem scarring observed in 1981 was not obvious in the second season. Unfortunately, assessment of current sprout mortality only occurred in 1982, although sprout mortality appeared higher in 1981. There are no quantitative data available to allow between-year comparisons.

9.1.1.3 Snowberry, Grass and Forb Yield

Annual production of western snowberry, grasses and forbs, in control clones, were compared for 1981 and 1982 (Table 17). Snowberry yield of current twigs, leaves and fruit was approximately doubled in 1982 over that measured in 1981, while the yield of grasses was reduced by almost 3 fold. The production of forbs was not significantly different between years of the study.

9.1.2 Discussion

The adaptation of snowberry to defoliation is well documented (Pelton 1953, Anderson and Bailey 1979, Anderson and Bailey 1980). Stems were significantly younger than root crowns indicating that clones of western snowberry should be aged from root crowns and not old stems. Although cattle were observed to make little use of snowberry clones in areas adjacent to the fenced study area, occasional trampling may explain the apparent juvenility of stems. Pelton (1953) reported that western snowberry stems were resilient to mechanical bending by heavy snow and glaze ice. On this study site, however,

[23]Identified by M.Y. Steiner, Alberta Agriculture.

Table 17. Annual dry matter yield of western snowberry[1], grasses and forbs (g/m^2) in control clones.

	1981	1982	S.E.
Snowberry	342a	628b	50
Grasses	150a	52b	11
Forbs	12a	26a	7

[1]Snowberry yield included new leaders, leaves and fruit.
[2]Means within rows followed by the same letter are not significantly different (Student-Newman-Keuls test, $p<0.05$).

especially during dormancy, stems appeared brittle and were easily broken. Pelton (1953) noted the presence of a fungal like material on young snowberry seedlings and further identified insects and drought as major causes of mortality. Results presented here are inconclusive, but mealy bugs may contribute to sprout mortality in regenerating snowberry stands. Whatever the causes of old stem and current sprout mortality, a high proportion of dead stems was evident and new sprouts had emerged to fill in the canopy.

It is possible that the apparent overturn of stems is indicative of a "fire type" adaptation in western snowberry. Fire adapted species tend to develop special characteristics which predispose them to combustion (Mutch 1970, Wright and Bailey 1982). One such adaptation may include the tendency to accumulate fuel as the stand becomes decadent (Gimingham 1971). The greater juvenility of stems versus root crowns and the high percentage of dead stems present may be evidence of such a fuel build up. Bailey and Anderson (1980) felt that higher fire temperatures in stands of western snowberry, as compared to adjacent grasslands, were related to the density of live and dead shrub stems. As stem density increased, so did fire temperature. Furthermore, fire temperatures within western snowberry stands were highest in the stand centres where the density of dead stems was greatest.

In light of the stem:root mass ratio of 1:1.3, defined here it would seem that the linear numerical ratio (1:4.4) described by Pelton (1953), may overemphasize the

relationship between above and below ground components.

Differences in climatic conditions, particularly precipitation, appear to explain the sizeable increase in shrub production during the second year. The increase in snowberry production was at the expense of understory grasses. Increased moisture levels may have increased the competitive advantage that western snowberry naturally possesses.

9.2 Appendix 2

A Analysis of the effect of different pH and temperature regimes on the yield of reducing sugars produced by alpha-amylase from freeze dried snowberry tissue.

Source	d.f.	S.S.	M.S.	F
pH	1	12.1	12.1	60.5**
Temperature	1	0.4	.4	4.0
pHxT	1	0.2	.1	.5
Tissue	2	20.0	10.0	50.0**
Error	30	6.7	.2	
Total	35	39.4		

B. Analysis of the effect of mowing on soil moisture in 1981 including grassland.

Source	d.f.	S.S.	M.S.	F
Date	4	17439.6	4359.9	262.6**
Treatment	8	620.1	77.5	4.7**
DxTreat.	32	725.5	22.6	1.4
Error	135	2243.0	16.6	
Total	179	21028.2		

C. Analysis of the effect of mowing on soil moisture in 1982 (Shrub versus fall mowed shrub).

Source	d.f.	S.S.	M.S.	F
Treatment	1	140.1	140.1	18.2**
Site	1	2085.1	2085.1	270.7**
TxS	1	0.2	0.2	.03
Horizon	1	38.6	38.6	0.5*
TxH	1	69.6	69.6	9.0**
SxH	1	688.1	688.1	89.4**
Date	12	652.5	54.3	7.1**
DatexT	12	36.8	3.1	.4
Error	97	754.1	7.7	
Total	103	3775.9		

D. Analysis of the effect of mowing on the origin of new shoots, sampled in 1982.

Source	d.f.	S.S.	M.S.	F
Treatment	6	24916.1	4152.6	6.85**
Error	68	41186.7	605.6	
Total	74	66102.9		

E. Analysis of the seasonal variation of NSC in three plant components, sampled from control clones in 1982.

Source	d.f.	S.S.	M.S.	F
Plant Component	2	2314.1	1157.1	57.4**
Clone	3	60.4	20.1	2.2
PCxC	6	54.5	9.1	2.9*
Date	11	602.3	54.7	7.8**
DxO	22	729.7	33.2	4.7**
CxD	33	229.5	6.9	2.3*
OxCxD	66	316.2	4.7	1.6*
Error	144	438.7	3.0	
Total	287	4745.5		

F. Analysis of the effect of date and treatment on the seasonal NSC pattern in control and spring mowed snowberry.

Source	d.f.	S.S.	M.S.	F
Treatment	1	204.9	204.9	9.2**
Clone/Tr.	6	134.2	22.3	12.1**
Date	11	880.2	80.0	2.8*
DxT	11	305.0	27.7	6.5**
DxCl/Tr.	66	281.7	4.2	2.3*
Error	96	177.7	1.8	
Total	191	1983.9		

G. Analysis of the effect of mowing on fall nonstructural carbohydrate reserves of snowberry in 1981.

Source	d.f.	S.S.	M.S.	F
Treatment	7	963.2	137.6	29.4**
Clones/Tr.	24	376.9	15.7	3.3**
Covariate	1	124.8	124.8	26.6**
Error	53	247.7	4.6	
Total	85	2316.2		

H. Analysis of the effect of mowing on autumn etiolated growth reserves of snowberry in 1981.

Source	d.f.	S.S.	M.S.	F
Treatment	7	417534.4	59647.7	7.3**
Clones/Tr.	24	365139.9	15214.1	1.8
Covariate	1	142223.3	142223.3	17.3**
Error	59	485057.7	8221.3	
Total	91	1538523.0	16906.8	

I. Analysis of the effect of mowing on a) total annual yield, b) fruit yield, c) stem density and d) plant density of snowberry and e) herbage in 1982.

a.

Source	d.f.	S.S.	M.S.	F
Treatment	7	15629540.6	2232791.5	22.0**
Clones/Tr.	24	2360467.3	98352.8	4.1
Error	288	6965593.9	24186.0	
Total	319	24955602.0		

b.

Source	d.f.	S.S.	M.S.	F
Treatment	7	350754.9	50107.8	8.7**
Clones/Tr.	24	137116.8	5713.2	10.8**
Error	288	152140.6	528.2	
Total	319	640012.4		

c.

Source	d.f.	S.S.	M.S.	F
Treatment	7	972486.3	138926.6	4.4**
Clones/Tr.	24	764154.0	31839.7	9.4**
Error	288	973249.6	3379.3	
Total	319			

d.

Source	d.f.	S.S.	M.S.	F
Treatment	7	9694.3	1384.9	2.9*
Clones/Tr.	24	11416.4	475.6	3.9**
Error	288	35192.0	122.1	
Total	319	56302.7		

e.

Source	d.f.	S.S.	M.S.	F
Treatment	7	851808.5	121686.9	13.1**
Clones/Tr.	24	222327.0	9263.6	3.4**
Error	288	780532.5	2710.2	
Total	319	1854668.1		